JOURNAL OF THE ROYAL SOCIETY OF NEW ZEALAND

Editor: Dr C. M. King
Publisher: SIR Publishing, PO Box 399, Wellington (incorporated within The Royal Society of New Zealand).

The *Journal of the Royal Society of New Zealand* is an independent, international, quarterly publication concerned with science in New Zealand or the Pacific region generally, including Antarctica. Its function is to record worthy scientific observations and debate, and to foster communication between (a) scientists working in different disciplines within New Zealand, and (b) scientists with similar interests working in different areas of the Pacific region. SIR Publishing does not, however, necessarily endorse any opinions expressed in the papers published in this journal.

We subscribe to the "Fair Copying Declaration" issues by the Royal Society of London. Reproduction, in full or in part, of author's abstracts is authorized provided the source is acknowledged. Permission to reproduce any other material, for purposes other than private study, must be obtained in writing from the Editor.

Notice to Contributors

1. Manuscripts must be submitted to the Editor, and specified as being intended for consideration as (a) an original research article; (b) a review or discussion paper; or (c) for the "Notes and Comments" section. MSS simultaneously submitted to SIR Publishing and to other Journals will not be considered.
2. Text should be typed double-spaced on one side only of A4-size paper. Underline generic and specific names if italic typeface is not available. Use international (SI) units wherever possible. Send two copies and keep an identical one.
3. Figures should be designed for final size of 13 × 20 cm or less. Lettering, hatching and symbols must be clear at this size and fully explained in the caption. Where possible, scale markings on the figure should be used instead of magnification ratios in the caption. Photographs must be glossy prints with sharp focus and good contrast. Label all figures on the back with their number and the author's name. All figures must have a caption, and be mentioned in order in the text. Small drawings should be collected together as a composite figure of suitable proportions, submitted as a glossy print or mounted on a clean white card. Send only two sets of A4-size copies of the figures in the first instance; originals may have to be returned for amendment after refereeing.
4. Tables should be numbered consecutively, referred to in order in the text, and designed to fit the print area of 13 × 20 cm. Only strictly necessary tables can be accepted.
5. References should be written out in full, without abbreviating journal titles. Give the title and the first and last page numbers of papers cited. "Personal communications" must be authorised by the person named, and dated. Unpublished papers should be cited as "In preparation", unless actually accepted for publication, in which case they may be cited as "In Press" in a named journal.
6. Proofs are sent to the author or senior author, for correction of typographical errors and updating of references. Changes in text introduced at this stage may be charged for.
7. Fifty free offprints are sent automatically to each author or group of authors. Extra offprints should be ordered when proofs are returned.
8. Authors alone are responsible for the accuracy of their data, conclusions, references, and quotations, and for obtaining permission to use material from other sources.
9. The MSS which pass most quickly through to press are those which are well thought out, written concisely and clearly and with careful attention to all important details of style, grammar, logic and numerical accuracy. Those authors who leave the editor and referees to do much of the work of organising and writing the MSS are the ones who are likely to suffer delays and disappointments. Intending contributors are urged to consult the *Guide to Contributors*, published in Volume 14, Number 1, pp. 107-118 (1984), which will help speed their MSS through with least trouble.

Journal of The Royal Society of New Zealand

Successor to the *Transactions* of the Society (1869-1971)

Volume 22, Number 2 **June, 1992**

CONTENTS

Original articles

Clarkson, B.R.; Clarkson, B.D.; Patel, R.N.: The pre-Taupo eruption (*c.* AD 130) forest of the Benneydale- Pureora district, central North Island, New Zealand 61–76
Keywords: buried forest, plant macrofossils, Taupo pumice, Dacrydium cupressinum, Phyllocladus trichomanoides, Metrosideros robusta, *radiocarbon dating, volcanic succession hypothesis*

Bussell, M.R.: Late Pleistocene palynology of terrestrial cover beds at the type section of the Rapanui Terrace, Wanganui, New Zealand 77–90
Keywords: pollen, Pleistocene, Rapanui Terrace, Rapanui Lignite, Rapanui Dunesand, Rapanui Formation, marine terraces, oxygen isotopes, vegetation history, climate, palaeoecology, biogeography, Acacia*-type*

Patterson, G.B.: The ecology of a New Zealand grassland lizard guild 91–106
Keywords: guild, Leiolopisma nigriplantare polychroma, Leiolopisma inconspicuum, Leiolopisma maccanni, *competition, home range, habitat preference, lizard, grassland, New Zealand*

Taylor, R.H.: New Zealand fur seals at the Antipodes Islands 107–122
Keywords: Arctocephalus forsteri, A. tropicalis, A. gazella, *exploitation, population recovery, population characteristics, breeding status, the Upland seal, Antipodes I., Macquarie I., Subantarctic*

Thompson, M.B.; Daugherty, C.H.; Cree, A.; French, D.C.; Gillingham, J.C.; Barwick, R.E.: Status and longevity of the tuatara, *Sphenodon guntheri*, and Duvaucel's gecko, *Hoplodactylus duvaucelii*, on North Brother Island, New Zealand 123–130
Key words: tuatara, Sphenodon guntheri, Sphenodon punctatus, *Duvaucel's gecko,* Hoplodactylus duvaucelii, *density, New Zealand, North Brother I.*

Damborenea, S. E.; Manceñido, M. O.: A comparison of Jurassic marine benthonic faunas from South America and New Zealand 131–152
Keywords: Palaeozoology, bivalves, brachiopods, Murihiku terrane, Andes, Early Jurassic (Aratauran, Ururoan), Middle Jurassic (Temaikan), Retroceramus, *New Zealand, Argentina, Chile, palaeogeography, Gondwanaland*

Beamish, B.B.; Vance, W.E.: Greenhouse gas contributions from coal mining in Australia and New Zealand 153–156
Keywords: coal mining, gas emission, greenhouse gases

Correction: Palma, R.L., in "A new species of *Rallicola* (Insecta: Phthiraptera: Philopteridae) from the North Island brown kiwi" 157

Published quarterly by SIR Publishing (incorporated within The Royal Society of New Zealand)

Previous issue (22/1) published 10 April, 1992 ISSN 0303-6758

THE ROYAL SOCIETY OF NEW ZEALAND

Founded 1867 as the New Zealand Institute; name changed, 1933.

President: Professor J. N. Dodd

Office of the Society: 4 Halswell Street, Wellington.
Telephone: Wellington (04) 472 7421: **Fax** (04) 473 1841.
Postal Address: The Royal Society of New Zealand, P.O. Box 598, Wellington, New Zealand

Publications

Volume 1 of the annual *Transactions and Proceedings of the New Zealand Institute* was published in 1869 (reprinted in revised form, 1875). The *Transactions* were published in quarterly parts from Volume 58 (1927-28) to Volume 88 (1960-61). A new volume numbering system and a division into sections (Zoology, Botany, Geology, and General) was instituted in 1961. In 1968, the number of sections was reduced to three (Biological Sciences, Earth Sciences, and General). Publication in this form, in which each paper was issued separately, was concluded at the beginning of 1971. This *Journal* is the successor to the *Transactions* of the Society and its predecessor, the New Zealand Institute. An author and title index to the complete run of the *Transactions* is available from the Society's offices ($10, $5 for members of affiliated societies).

The annual *Proceedings* of the Society (formerly included with the *Transactions*) have been published separately from Volume 85 (1958). They include a full account of the Society's activities, names and addresses of Fellows and honorary members, personnel and reports of committees, the Council's annual report, annual reports of member bodies, details of the Society's medals and prizes with lists of medallists and prize-winners, trust and other funds, research grants and reports of grant recipients, occasional special articles, and obituaries. They also list the current honorary and paid officers of the Society. The Royal Society of New Zealand Act (1965), amending the 1933 Act, and the Rules adopted under the authority of the Act were last published in the *Proceedings* for 1968-69; a current set of rules is available from the Society's offices.

Bulletins of the Society consist of works of scientific research that are considered unsuitable, because of size or content, for publication in the *Journal*. They are published at irregular intervals, subject to the approval of the Council in each instance.

The Society also publishes a *Miscellaneous Series*, which in general includes reports of special committees established by the Society's Council. These are also issued at irregular intervals.

Selected publications available from the Society are described on the inside back cover of this journal.

On 1 July 1991, The Royal Society of New Zealand acquired the publishing unit of the Department of Scientific and Industrial Research (DSIR) and renamed it Scientific and Industrial Research Publishing of New Zealand (SIR Publishing). The *Journal of The Royal Society of New Zealand* is now published by this unit together with the six other research journals inherited from DSIR (refer inside rear cover) and other miscellaneous publications.

© Copyright The Royal Society of New Zealand 1992
Printed by Wright and Carman Ltd., Upper Hutt, New Zealand.

© *Journal of the Royal Society of New Zealand,*
Volume 22, Number 2, June 1992, pp 61–76

The pre-Taupo eruption (*c.* AD 130) forest of the Benneydale-Pureora district, central North Island, New Zealand

Beverley R. Clarkson*, Bruce D. Clarkson and Rajni N. Patel*****

The composition and structure of three small areas of west Taupo forest, blasted down and buried during the *c.* AD 130 Taupo tephra eruption, are revealed by analysis of plant macrofossils, including leaves, seeds and wood. Data from these three sites and from the recently described Pureora buried forest were then used to interpret the pre-eruption vegetation along a 20 kilometre transect, from Pureora westward to Benneydale. All the stands were on flat or undulating terrain and dominated by podocarps, ranging from rimu (*Dacrydium cupressinum*)-tanekaha (*Phyllocladus trichomanoides*) at Pureora to rimu at Benneydale. Broadleaved trees increased westward; on lower hillslopes in the Benneydale buried forest, northern rata (*Metrosideros robusta*) was an important canopy component. An amelioration of climate with decreasing altitude westward was indicated by a gradual change from prominence of horopito (*Pseudowintera colorata*) at Pureora to *P. axillaris* at Benneydale, and the presence of rewarewa (*Knightia excelsa*) and *Metrosideros perforata* only at the Benneydale site. In the extant forests adjacent to the sites, the broadleaved tree species, tawa (*Beilschmiedia tawa*), kamahi (*Weinmannia racemosa*) and mahoe (*Melicytus ramiflorus* ssp. *ramiflorus*) are common, but these were not recorded in any buried forest. Classification and ordination techniques were applied to data from three buried forest sites, approximately 10 km apart along the transect. These arranged the plots and species in a spatial sequence from Pureora to Benneydale, and also reflect a gradient from very poor to comparatively better drainage. The volcanic succession hypothesis of McKelvey (1963, 1986) is discussed in light of the macrofossil data. Our evidence suggests that broadleaved, notably tawa, forest is not the endpoint of the forest succcession on flat to undulating sites, and that forests may not converge to the extent suggested by McKelvey. We postulate that, under the present climate regime, and in the absence of volcanic eruptions and logging, the podocarp species which were widespread in the buried forests will eventually dominate terrain of gentle relief in the Pureora-Benneydale district.

Keywords: buried forest, plant macrofossils, Taupo pumice, Dacrydium cupressinum, Phyllocladus trichomanoides, Metrosideros robusta, *radiocarbon dating, volcanic succession hypothesis*

INTRODUCTION

Macrofossils preserved among the remains of forest near Pureora which was overwhelmed and buried during the *c.* AD 130 (Froggatt, 1981) Taupo eruption were described by Clarkson, Patel and Clarkson (1988). We also made additional studies of three other buried forests in the district. Our aim was to determine the pre-Taupo forest pattern over a wider area, and to use these data to further refine hypotheses presented in our earlier paper. We also appreciated the opportunity to examine the composition of forests pre-dating humans and introduced animals.

---

* 13 Melrose Avenue, Rotorua.
** DSIR Land Resources, C/- FRI, Private Bag 3020, Rotorua.
*** DSIR Land Resources, Private Bag, Christchurch.
Please address requests for reprints to Bruce D. Clarkson.

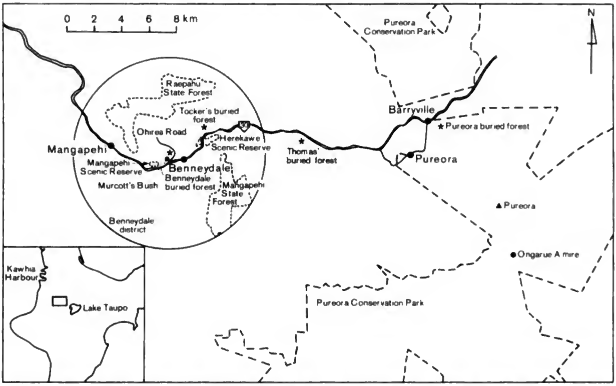


Fig. 1 - Map showing Benneydale, Tocker, Thomas, and Pureora buried forest locations. Benneydale district (area within 7 km of Benneydale buried forest site) is represented by the circle.

STUDY AREAS

We sampled plant macrofossils from three buried forest sites which, together with the already-described Pureora site, were located along a 20 km transect from Pureora westward to Benneydale (Fig. 1). The study began in August 1986 and was concentrated at Benneydale, where the most extensive and best preserved forest was found.

The Benneydale buried forest was discovered during ditch digging over 40 years ago and in 1985 was placed under an open space covenant with the Queen Elizabeth II National Trust, protecting the site for scientific investigation. A preliminary study of the leaves and wood in the early 1950s by Mr A.E. Beveridge indicated the well-preserved remains of a podocarp forest dominated by rimu (*Dacrydium cupressinum*); five wood samples from logs exposed in the ditches were identified as *Nestegis* sp., rimu, *Metrosideros* sp., totara (*Podocarpus totara*) and kahikatea (*Dacrycarpus dacrydioides*) (Pullar and Patel, 1972).

The site is 1.9 ha in area and situated adjacent to Ohirea Road, 1 km north of Benneydale township, at 350 m a.s.l. (Fig. 2). It occupies a small saddle between rolling hills, on terrain which is mainly flat but rising gently in the south-west corner. Present vegetation comprises pasture grasses with rushes (mainly *Juncus effusus*) in the central portions where drainage is impeded, and scattered manuka (*Leptospermum scoparium*) and blackberry (*Rubus fruticosus* agg.) along parts of the ditches and fenceline. The yellow brown pumice soil is about 15 cm thick and overlies *c.* 1.2 m of Taupo pumice flow tephra comprising a *c.* 0.6-0.9 m lower layer of Taupo pumice and a *c.* 0.6 m upper layer of pumice alluvium derived from the tephra (Pullar and Patel, 1972). The buried forest soil was found immediately beneath the pumice with litter and abundant fibrous roots in the upper horizons and a gleyed lower uB horizon (Pullar and Patel, 1972). At least 200 cm of older weathered unidentified ash lies between the old soil and the country rock, mudstones and sandstones of the Miocene Mohakatino Group (Hay, 1967). The mean annual temperature at the site is *c.* 12.5°C (New Zealand Meteorological Service, 1985) and the mean annual rainfall, calculated from a simple regression equation based on data from three nearby climatological stations located approximately parallel to the

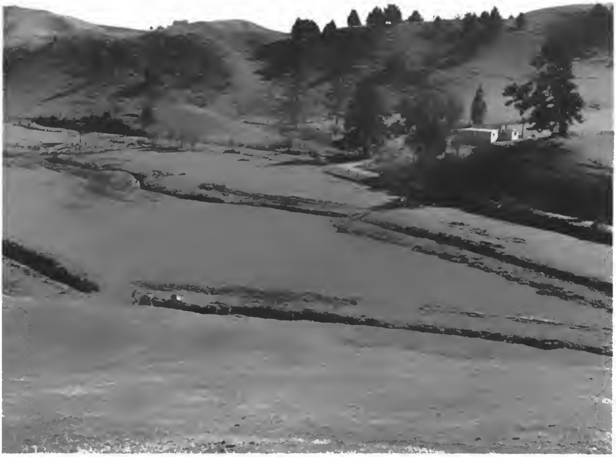


Fig. 2 - View, looking northwards, of Benneydale buried forest site showing ditches. Ohirea Road is in the background.

transect (New Zealand Meteorological Service, 1973) is *c.* 1681 mm. Remnants of indigenous forest close to the site include 'Murcott's Bush' (also covenanted with Queen Elizabeth II National Trust; 8 ha), Herekawe (234 ha) and Mangapehi (46 ha) Scenic Reserves, Mangapehi and Raepahu State Forests, and numerous scattered unprotected patches.

'Tocker buried forest' was discovered under 3-4 m of Taupo pumice alluvium during culvert construction in 1985, at a flat site 4 km north-east of the Benneydale site, at 396 m altitude. The extant vegetation is mainly exotic pasture grasses with scattered patches of indigenous scrub and forest. Preservation of macrofossils at this site was generally poor due to oxidation resulting from exposure.

'Thomas buried forest' was found beneath *c.* 4 m of Taupo pumice alluvium during recent dam construction on a small stream, 457 m altitude, approximately halfway between the Benneydale and Pureora buried forests. Surrounding vegetation was mainly pasture, with some indigenous scrub lining the banks of the upper Waimiha Stream and tributaries.

All three sites supported similar vegetation around 1912, before clearance for farming (J. Murcott, pers. comm. 1989). On the flats where the pumice was deep and unconsolidated, manuka was dominant, growing with monoao (*Dracophyllum subulatum*), and occasional cabbage tree (*Cordyline australis*), with kanuka (*Kunzea ericoides*) along stream banks. Away from the flats on the lower hillslopes, tree ferns *e.g. Cyathea smithii*, then kamahi (*Weinmannia racemosa*) became prominent, giving way, on the mid slopes, to mostly tawa (*Beilschmiedia tawa*) dominated forest overtopped by the podocarps rimu, matai (*Prumnopitys taxifolia*) and totara. Rewarewa (*Knightia excelsa*) was also common in places. At the Benneydale buried forest site the surrounding undulating country and slopes down to the stream terrace had emergents of (in order) rimu, totara, matai and miro (*Prumnopitys ferruginea*) scattered over a mainly tawa canopy (probably type M8; rimu/tawa forest of McKelvey (1963)).

Along the 20 km transect, from Pureora to Benneydale, altitude decreases by 200 m, mean annual temperature increases by *c.* 2.2°C and annual rainfall decreases by *c.* 148 mm. Pureora, the most inland and climatically severe location, displays some continentality in its temperature ranges; extremes of 30°C and -9°C have been recorded (Hessell, 1986). Although thick at all sites, the overlying pumice thins out westward; strongly podzolised yellow-brown pumice soils (Tihoi series) are characteristic around Pureora, and moderately podzolised yellow-brown pumice soils on yellow-brown loams (Ngaroma series) at Benneydale (Rijkse and Wilde, 1976). The unmodified indigenous vegetation along the transect from east to west ranges from dense mixed podocarp forest (type L1) dominated by matai and rimu, to podocarp/tawa forest (type M2) to rimu/tawa forest (type M8) to rimu/tawa/northern rata forest (type D1) (McKelvey, 1963).

METHODS

The litter sampling procedure followed Clarkson *et al.* (1988) except that the sampling interval was halved to 5 m because of the small site areas and the rejection of numerous samples with poorly-preserved litter. Leaf litter cover scores of 1 to 7 were allocated for each species, and species lists were compiled for all sites. Of the 79 Benneydale samples collected and sorted, 51 had litter sufficiently preserved for analysis; similarly, only two Thomas samples out of six collected from Tocker and Thomas buried forests were suitable. Classification and ordination analyses using the programmes TWINSPAN and DECORANA (Hill, 1979a, 1979b), were carried out on first, the Benneydale data, and second, the combined Pureora (Clarkson *et al.*, 1988), Thomas and Benneydale data, to help identify trends in floristic composition.

Thirty wood samples from Benneydale were obtained from the ditches and identified in the manner described in Clarkson *et al.* (1988). No wood was collected from the other two sites, because none was accessible and well-preserved. In addition, about 200 seeds, including fruit, of toro (*Myrsine salicina*) from the Benneydale samples were submitted to the Institute of Nuclear Sciences, DSIR, Lower Hutt, for radiocarbon dating to obtain a Taupo eruption date using material that pre-dated the event by less than one year.

An attempt was made to try to detect possible signs of moa browsing and other indigenous animal (including insect) damage on the macrofossil leaves and twigs.

RESULTS

Benneydale, Tocker and Thomas buried forests

Twenty-nine vascular species, comprising 19 trees and shrubs, four lianes, six ferns and one sedge, were identified from the Benneydale leaves, seeds and wood (Table 1; Fig. 3). Eleven and ten species, respectively, were identified from the leaves collected at Tocker and Thomas buried forests, which include two ferns (*Leptopteris superba*, *Blechnum* sp. (*B. capense* agg., lower pinnae reduced)) and one shrub (horopito, *Pseudowintera colorata*) additional to the Benneydale list. Six tree species, rimu, northern rata (*Metrosideros robusta*), narrow-leaved maire (*Nestegis montana*), tanekaha (*Phyllocladus trichomanoides*), miro, and matai, were recorded at all three sites.

Eight species were identified from the Benneydale wood samples (Table 2A), of which rimu (53% occurrence), miro (13%), and northern rata (10%) were the three most abundant. A single *Libocedrus* log was recovered but it could not be confidently ascribed to either kaikawaka (*L. bidwillii*) or kawaka (*L. plumosa*); photomicrographs suggested greater similarity with kaikawaka. Analysis of the leaf litter cover of the ten species recorded in more than 20 samples at Benneydale (Table 2B) showed that rimu, *Metrosideros diffusa*, miro, northern rata, crown fern (*Blechnum discolor*) and toro (*Myrsine salicina*) were represented in more

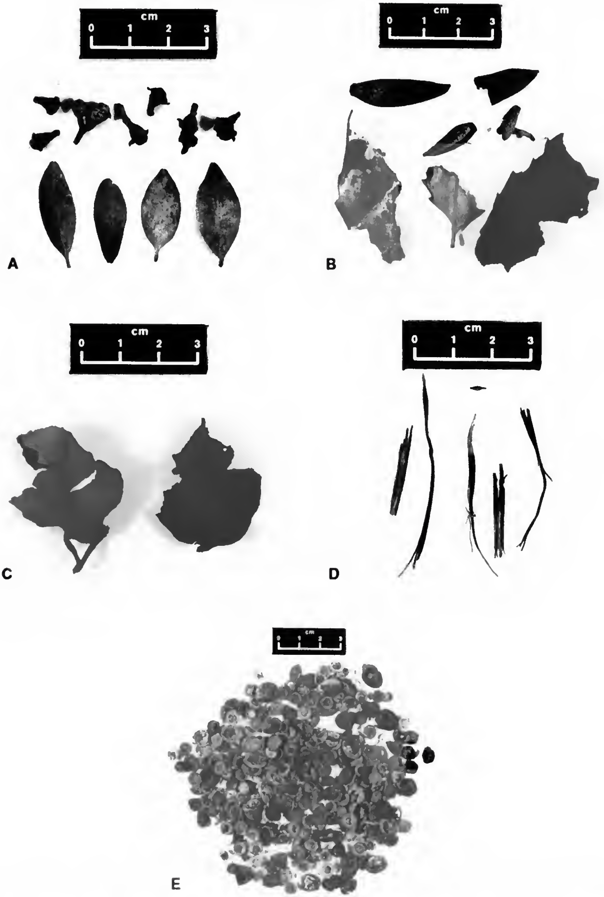


Fig. 3 - Examples of plant macrofossils recovered from Benneydale buried forest. A. Northern rata (*Metrosideros robusta*); B. Rewarewa (*Knightia excelsa*); *C. Rubus australis*; *D. Uncinia* sp. *zotovii*?; E. Seeds - mainly matai (*Prumnopitys taxifolia*) and miro (*P. ferruginea*)

Table 1 - List of species from Benneydale, Tocker and Thomas buried forests collated from recovered leaves, seeds and wood

Vascular species	Benneydale				Tocker leaves	Thomas leaves
	Leaves	Seeds	Wood	Overall abundance		
Blechnum discolor	c			c		r
B. sp. (B. capense agg. common sp. lower pinnae reduced)					r	
Ctenopteris heterophylla	r			r		
Cyathea smithii	o			o		
Dacrycarpus dacrydioides	o	o		o		
Dacrydium cupressinum	a	a	a	a	a	a
Dicksonia squarrosa	o	o				
Dracophyllum sp. *(subulatum?)*	r			r		r
Elaeocarpus dentatus		r		?		
E. hookerianus	r	r		r	r	
Hymenophyllum demissum	r			r		
Knightia excelsa	o	o2	r	o		
Leptopteris superba						o
Libocedrus sp.			r	r		
Metrosideros diffusa	c	c2		c	r	
M. fulgens	r			r		
M. perforata	o			o		
M. robusta	a	c2	o	c	r	r
Myrsine salicina	c	a		c		
Neomyrtus pedunculata	r		r			
Nestegis cunninghamii	r	o	o3	r		
N. lanceolata	r	o	o3	r	r	
N. montana	o	o	o3	o	o	r
Phyllocladus trichomanoides	o1		r	o	c	c
Podocarpus totara	r		o4	r	r	
Prumnopitys ferruginea	c	c*	o	c	o	o
P. taxifolia	o	o*		r	r	r
Pseudowintera axillaris	c	o		c	?	?
P. colorata						c
Rubus australis	o			o		
Uncinia sp. (zotovii?)	o	r		o		
Unidentified fern	r			r		
Total				29	11	10

* Hundreds of mainly matai and miro seeds were uncovered at one site but have not been included in the seed abundance ratings.
Key: a = abundant; c = common; o = occasional; r = rare
1 = phylloclades; 2 = capsules; 3 = identified to genus only; 4 = identified as *Podocarpus hallii* or *P. totara*

than 80% of the samples. These ten species collectively accounted for 85% of the total leaf litter cover; rimu, northern rata, crown fern and toro recorded 21%, 11%, 9% and 9% respectively.

A profile diagram was derived from litter and log data from four consecutive sample sites in the south-western ditch at the Benneydale site (Fig. 4), in a manner similar to that described in Clarkson *et al.* (1988). This typifies the forest composition and structure on the gently rising south-west hill slopes; northern rata becomes less frequent northwards on the

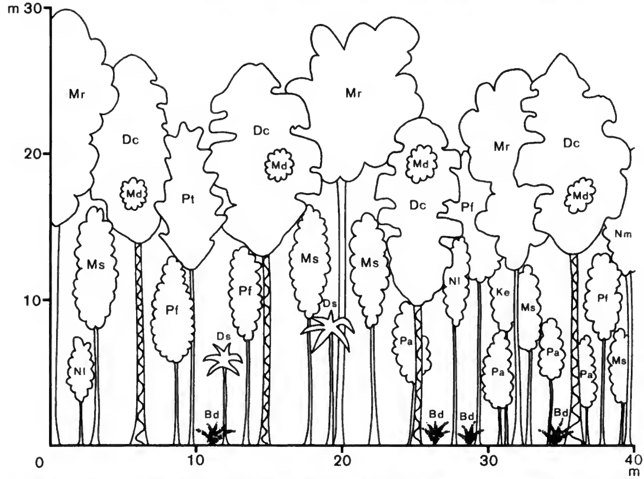


Fig. 4 - Profile of forest derived from litter and log data from four consecutive ditch sites located in the south-west corner of Benneydale buried forest site. Approximate area is 600 m^2. Bd = *Blechnum discolor*; Dc = *Dacrydium cupressinum*; Ds = *Dicksonia squarrosa*; Ke = *Knightia excelsa*; Md = *Metrosideros diffusa*; Mr = *Metrosideros robusta*; Ms = *Myrsine salicina*; Nl = *Nestegis lanceolata*; Nm = *Nestegis montana*; Pa = *Pseudowintera axillaris*; Pf = *Prumnopitys ferruginea*; Pt = *Phyllocladus trichomanoides*

Table 2A - Occurrence of tree species determined from wood samples; Benneydale buried forest

Species	Total occurrence	Percent occurrence
rimu	16	53
miro	4	13
northern rata	3	10
Nestegis sp.	2	7
totara	2	7
tanekaha	1	3
Libocedrus sp.	1	3
rewarewa	1	3
	30	100

Table 2B - Leaf litter frequency and relative cover of species recorded in more than 20 samples; Benneydale buried forest

Species	Frequency	Average cover score*	Percent cover
rimu	51	3.1	21
Metrosideros diffusa	50	1.2	8
miro	49	1.1	7
northern rata	44	2.0	11
crown fern	43	1.5	9
toro	41	1.7	9
kahikatea	34	1.2	5
Pseudowintera axillaris	27	1.7	6
rewarewa	27	1.3	5
tanekaha	24	1.4	-
N = 51			85

* Average cover score = $\frac{\text{sum of cover scores}}{\text{total samples}}$

flatter terrain. The canopy at *c*. 30 m was dominated by rimu and northern rata, whose log diameters ranged from about 30 cm to more than 1 m. Other canopy species included occasional tanekaha, miro, kahikatea, totara, narrow-leaved maire, white maire (*Nestegis lanceolata*), black maire (*N. cunninghamii*), rewarewa and *Libocedrus* sp. Toro and miro probably dominated the subcanopy, and *Pseudowintera axillaris*, wheki (*Dicksonia squarrosa*), *Cyathea smithii* and *Neomyrtus pedunculata*, the shrub layer. The most common ground cover was crown fern; only two other ground cover species, *Uncinia* sp. (*zotovii*?) and *Hymenophyllum demissum* (also epiphytic), were identified. Lianes present were *Metrosideros diffusa*, *M. perforata*, *M. fulgens* and *Rubus australis*.

Radiocarbon dating of the toro seeds gave a figure of 1795 ± 55 yr BP (Radiocarbon Number 11408, Libby T1/2 (5568 yr)).

There was no conclusive evidence of browsing of leaves and twigs by moas; the macrofossils were extremely brittle and few leaves were recovered whole. Damage caused by browsing insects, however, was prevalent. For example, small holes in *Metrosideros diffusa* leaves resemble damage caused by present day adult *Neomycta rubida* weevils, and altered leaf margins of *Pseudowintera* spp. suggest the presence of lepidopterous larvae or coleopteran adults (J. A. Hutcheson, pers. comm., 1991).

The classifications and ordinations of the Benneydale site data indicated a relatively uniform forest with minor variation reflected by the distribution and abundance of the two dominant species, rimu and northern rata. This variation mainly accords with the slight variation in topography, since northern rata increases in abundance towards the gentle slopes to the south-west. The relationship between the two groups delimited by the plot classification and the dominant species at each sample is depicted on the sample ordination (Fig. 5). Group 1 comprises plots dominated by, or with a high component of, northern rata, and have a low score on Axis 1, whereas Group 2 plots are dominated by rimu and have a high score on Axis 1.

Classification and ordination; Benneydale, Thomas and Pureora buried forests

Classification of the combined Benneydale, Thomas and Pureora plots at Level 2 delimited four ecologically recognisable groups (Table 3: Atkinson, 1985) arranged in a spatial sequence from Pureora to Benneydale. Group 1, Rimu-tanekaha/*Astelia grandis* tussockland comprised eight Pureora plots and was similar to the group with the same name produced by the Pureora buried forest classification (Clarkson *et al*., 1988). It represented poorly-drained tussocklands of *Astelia grandis* and *Gahnia xanthocarpa*, with scattered small-stemmed rimu, tanekaha and kahikatea to the south of the site. Group 2, Rimu-tanekaha forest, was made up of 44 plots with high components of rimu and tanekaha. Other typical species were matai, miro, kahikatea, narrow-leaved maire, toro, horopito, *Neomyrtus pedunculata*, *Metrosideros diffusa* and crown fern. Drainage was probably impeded in places because of the occasional presence of mire species such as *G. xanthocarpa* and, to a lesser extent, bog pine (*Halocarpus bidwillii*) and *A. grandis*. This large group consisted of 40 Pureora, two Thomas, and two Benneydale plots. Group 3, Rimu forest, was made up of 28 Benneydale plots dominated by rimu, with other species including miro, rewarewa, toro, *Pseudowintera axillaris*, *M. diffusa* and crown fern. Twenty-one plots co-dominated by rimu and northern rata from the better-drained south-west slopes of Benneydale formed Group 4, Rimu-northern rata forest. Typical associates were miro, toro, *P. axillaris*, *M. diffusa* and crown fern.

The species classification resulted in five groups (Table 3) which formed a gradation from species typical of poorly-drained sites, *e.g*., *G. xanthocarpa*, *A. grandis*, to those found in better-drained sites, *e.g*., northern rata, rewarewa. Ordination techniques also arranged the plots and species in a sequence from tussockland to forest, following drainage and climatic gradients. Both correspond with a geographical sequence from Pureora to Benneydale reflecting an amelioration of climate from the high centre towards the periphery of the volcanic plateau (see above on Study areas for details).

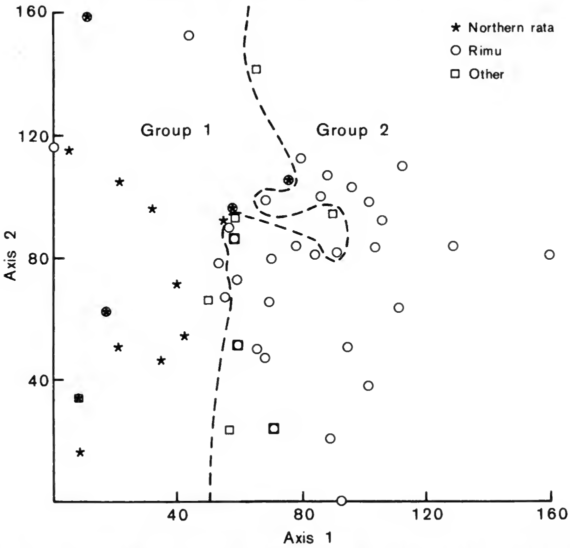


Fig. 5 - A two-dimensional plot ordination of the first two axes of a DCA ordination combined with the two groups defined by Level 1 of a TWINSPAN normal (plot) classification, Benneydale buried forest. A symbol representing the dominant at each plot has been overlaid.

Comparison between Benneydale buried forest and present day forest

Ideally, past/present forest comparisons should involve adjacent sites on similar terrain (as in the Pureora buried forest/Pikiariki Ecological Area comparison; Clarkson *et al.* 1988). Unfortunately, little native vegetation remains on flat to gently undulating land close to the Benneydale buried forest site. The nearest remnant is Murcott's Bush (Fig. 1), about 100 m south-west, but the terrain there is moderately steep, with only minor gentle lower hillslope similar to that of the buried forest. However, the forest throughout Murcott's Bush is relatively uniform and is similar to forest that existed on adjacent undulating land before clearance early this century (see STUDY AREAS). It is compared with that of the Benneydale buried forest in Table 4.

Murcott's Bush was, along with other unprotected remnants in the Benneydale district, logged for podocarps, mainly rimu, before 1945 (as deduced from aerial photographs). Before logging it had a scattered overstorey of rimu (averaging 10 per ha, type M8, rimu/tawa forest; McKelvey, 1963) and a dense lower tier dominated by tawa (*Beilschmiedia tawa*), with occasional rewarewa, hinau (*Elaeocarpus dentatus*) and kamahi (*Weinmannia racemosa*). The Benneydale buried forest was a dense podocarp forest, perhaps up to 125

Table 3 - Classification of samples and species; Benneydale, Thomas and Pureora buried forests. Group cover values for each species have been averaged as a relative index for cover abundance

Species	Classificatory sample groups*				Species group
	1	2	3	4	
Halocarpus bidwillii	0.3	0.1			
Astelia grandis	2.5	0.2			
Freycinetia baueriana ssp. *banksii*	0.8	0.1			A
Coprosma sp. (t)	0.1	+			
Gahnia xanthocarpa	1.1	0.5			—
Neomyrtus pedunculata	0.1	0.7	+		
Eleaocarpus hookerianus		0.2	+		
Prumnopitys taxifolia	0.3	1.0	0.1	0.1	
Pseudopanax anomalus		0.1			
Pseudowintera colorata		1.5			B
Leptopteris superba		0.2			
Pseudopanax crassifolius		0.1			—
Phyllocladus trichomanoides	2.0	2.1	0.7	0.6	
Nestegis montana	0.6	0.6	0.4	0.1	C
Podocarpus totara		0.1	0.1		—
Cyathea smithii	0.1	0.2	0.4		
Dacrycarpus dacrydioides	1.8	0.8	1.0	0.6	
Dacrydium cupressinum	2.6	3.1	3.9	2.8	
Metrosideros diffusa	0.1	0.9	1.3	1.0	
Myrsine salicina	0.6	1.3	1.3	1.4	D
Prumnopitys ferruginea	0.9	1.1	1.1	1.0	
Blechnum discolor	0.3	0.9	1.6	0.8	—
Metrosideros robusta	0.3	0.3	1.0	2.8	
Dicksonia squarrosa		0.1	0.3	0.2	
Rubus australis	0.4	0.1	0.2	0.2	
Nestegis cunninghamii			+	0.3	
Nestegis lanceolata			0.1	0.3	
Metrosideros fulgens				0.1	E
Hymenophyllum demissum		0.1	0.2	0.1	
Uncinia zotovii	0.1	0.1	0.4	0.1	
Metrosideros perforata		+	0.4	0.2	
Pseudowintera axillaris			1.2	0.7	
Knightia excelsa		+	0.9	0.5	
Ctenopteris heterophylla			0.1		
Number of samples	8	44	28	21	

* Sample group names
Group 1: Rimu-tanekaha/*Astelia grandis* tussockland
Group 2: Rimu-tanekaha forest
Group 3: Rimu forest
Group 4: Rimu-northern rata forest

stems per ha, dominated by rimu, with frequent miro (equivalent to type L1 of McKelvey, 1963), but also comprising locally frequent northern rata.

Eight of the ten leading dominant species in Murcott's Bush, *i.e.*, tawa, kamahi, mahoe (*Melicytus ramiflorus* ssp. *ramiflorus*), *Rhabdothamnus solandri*, *Blechnum chambersii*, *Leptopteris hymenophylloides*, *Pneumatopteris pennigera* and supplejack (*Ripogonum scandens*), were not recorded in the buried forest. These species are also relatively common

Table 4 - Comparison of leading dominant species in Benneydale buried forest and Murcott's Bush

Forest layer	Benneydale buried forest (*c.* AD 130)	Murcott's Bush (AD 1986)
Canopy	rimu	tawa*
	northern rata	rewarewa
	miro	hinau
		kamahi*
		(rimu)
Subcanopy	toro	mahoe*
	miro	tawa*
Shrub	*Pseudowintera axillaris*	*Rhabdothamnus solandri**
	wheki	
Ground	crown fern	*Blechnum chambersii**
		*Leptopteris hymenophylloides**
		*Pneumatopteris pennigera**
Liane	*Metrosideros diffusa*	supplejack*

NB Species are ranked in order of cover abundance for each layer (*i.e.* tawa most abundant in Murcott's Bush canopy, rewarewa second most abundant *etc.*). The buried forest rankings were based on litter and log data, whereas Murcott's Bush rankings were from cover estimates.

* Not recorded in Benneydale buried forest.

( ) Now mostly logged

in other contemporary forest remnants in the Benneydale district, *e.g.* Herekawe and Mangapehi Scenic Reserves. In contrast, all eight dominant buried forest species listed in Table 4 are nowadays found within the Benneydale district, although toro is generally found at altitudes higher than the buried forest site.

The closest forest on flat to undulating terrain is on private land, 4 km south-west of the Benneydale buried forest. There, before logging, scattered large northern rata, rimu and matai were emergent over a dense tawa canopy (type D1, rimu/tawa/northern rata forest of McKelvey, 1963; from National Forest Survey database). But again, this forest had abundant tawa, mahoe and kamahi, plus all other Murcott's Bush species listed in Table 4, so was dissimilar in composition to the Benneydale buried forest.

Of the 29 species recorded in the Benneydale buried forest, *Libocedrus* sp,. and perhaps tanekaha are not found nearby today. Tanekaha grows in Pureora Conservation Park, *c.* 15 km north-east of the site (from National Forest Survey database), and maybe closer. The nearest record of kaikawaka is 36 km south-east in Whenuakura Ecological Area, whereas that of kawaka is probably near Kawhia Harbour, *c.* 60 km north-west.

An edaphic L1 subtype, matai/miro/totara-dominant dense mixed podocarp forest, is described by McKelvey (1963) for the wider west Taupo area. This subtype represents extant forest which grows mainly on alluvial flats and easy terrain with thick pumice deposits, and in scattered patches along river flats around Benneydale. However, although this contemporary type is found on terrain similar to that of the Benneydale buried forest, it differs in composition; it is dominated by matai, with frequent to co-dominant miro and totara, and only occasional rimu. Other common trees include *Nestegis* spp., pokaka (*Elaeocarpus hookerianus*), toro, *Fuchsia excorticata*, kamahi, putaputaweta (*Carpodetus serratus*) and mahoe (*Melicytus ramiflorus* ssp. *ramiflorus*); the four last-mentioned species were not recorded in the buried forest.

Comparison between Benneydale, Tocker, Thomas and Pureora buried forests

The four sites sampled all formerly supported dense podocarp forest dominated by rimu, but we distinguish trends in species abundance along the 20 km transect. Tanekaha and matai, the second and third dominant respectively in the easternmost, Pureora, buried forest (Clarkson *et al.*, 1988), declined in abundance westward to the Benneydale site. On the other hand, northern rata, rare in the Pureora buried forest, became commoner towards Benneydale, and attained second dominance there. Horopito (*Pseudowintera colorata*) was the main shrub in Pureora and Thomas buried forests, whereas at Benneydale it was *Pseudowintera axillaris*. Miro remained relatively common at all four sites. Toro was prominent at both ends of the transect, but not recorded at either the Tocker or Thomas sites. This absence, and those of other species at the two middle sites, may merely be a function of the smaller areas sampled there. Trends in shrub, ground layer and liane species were probably masked by their poorer litter:live matter correlation (see Clarkson *et al.*, 1988), but crown fern and *Metrosideros diffusa* were generally common throughout.

Comparison between the buried forests at the two extremes of the transect revealed significant differences in species composition. Six species, *Ctenopteris heterophylla*, monoao, rewarewa, *Metrosideros fulgens*, *M. perforata* and black maire were recorded only at Benneydale, whereas 16 species were recorded only at Pureora. At least eight of these species, *e.g.*, *Astelia grandis*, *Gahnia xanthocarpa*, and bog pine were associated with mire patches concentrated at the southern end of the Pureora site; there were no similar patches at Benneydale.

Tocker buried forest was very similar in composition to the Benneydale buried forest, but Thomas, with its high abundance of horopito and *Leptopteris superba*, was more closely allied to Pureora. This was borne out by the results of the sample classification (Table 3).

All four buried forests lacked the broadleaved species tawa, kamahi, and mahoe, which are common trees in the central North Island today. Also, few of the shrub and ground layer species typical of present day forests adjacent to the sites were recorded in any of the buried forests.

DISCUSSION

Differences in species composition and abundance in the Benneydale and Pureora buried forests are probably due to differences in climate and soils. Species that require relatively warm climates, *e.g.*, rewarewa and *Metrosideros perforata*, were recorded at Benneydale, but not at the higher-altitude, more inland Pureora site. *Pseudowintera axillaris* and horopito, the dominant shrubs at Benneydale and Pureora respectively, are usually separated altitudinally in the central North Island at present; *P. axillaris* is found at the lower altitudes. The higher species number recorded at Pureora is mainly the result of a greater habitat range allowed by the interspersed herbaceous and shrub mire patches, and also the larger area that was sampled there than at Benneydale.

The buried forests represent only alluvial flat, gentle undulation, lower hillslope, or poorly-drained variants of the regional forests that were present before the Taupo eruption. As such they can be compared directly only with forests which grow on similar terrain, *i.e.* the edaphic subtype of the dense mixed podocarp type L1, matai-miro-totara-dominant dense mixed podocarps, and some rimu/tawa (M8) and rimu/tawa/northern rata (D1) types (of McKelvey, 1963). There are significant differences in composition and abundance between then and now, most notably in the greater abundance in the buried forests of rimu and tanekaha, the presence of *Libocedrus*, and the absence of tawa, kamahi and mahoe. The ecological characteristics of the buried forest species suggest that the pre-Taupo soils were of low fertility, whereas the abundance of tawa and mahoe on contemporary topograhically-equivalent sites indicates higher levels of fertility (see Clarkson *et al.*, 1988).

Although the absence of tawa, mahoe and kamahi from all buried forests may be partly explained by pre-Taupo/post-Taupo differences in soils, the four sites were topographically similar; all were flat or gently undulating. These sites would have probably favoured podocarps over broadleaved species irrespective of the neighbourhood seed source. Thus 'missing' species may well have been growing on better-drained, more fertile hills or hillslopes in the vicinity. No tawa seeds, which are large and bird-dispersed, were found in the buried forests, although tawa fruit crops fluctuate considerably from year to year (Knowles and Beveridge, 1982). On the other hand, hinau seeds, also large and bird dispersed, were recorded in both Benneydale and Pureora buried forests, yet the species was unrepresented in the litter and wood.

To supplement the macrofossil data, particularly with respect to 'missing' species, pollen diagrams, representing the vegetation of large areas, were constructed from cores taken at the Pureora and Benneydale sites. These revealed no *Beilschmiedia, Melicytus* or *Weinmannia* pollen in layers dating from immediately before the Taupo eruption (M. S. McGlone, unpublished data). Tawa and, to a lesser extent, mahoe pollen, however, are severely underrepresented in modern pollen rain, but kamahi is generally well-represented (Bussell, 1988). Therefore, while it can be assumed that kamahi was probably absent from the buried forest vicinity, the same cannot be said about tawa and mahoe, although these species are considerably more abundant now.

The presence of a single *Libocedrus* log in Benneydale buried forest supports the suggestion of Clarkson *et al.* (1988) that *Libocedrus* had declined in abundance since a peak in the early post-glacial period (see also McGlone and Topping, 1977) and became locally extinct as a result of the Taupo eruption.

The stages of development of seeds and/or fruit recovered from the Benneydale buried forest were similar to those from the Pureora buried forest, thus supporting the estimated (Clarkson *et al.*, 1988) Taupo eruption time of late summer. The radiocarbon date of 1795 ± 55 yr BP was one of 41 used to calculate a mean radiocarbon age for the Taupo Tephra Formation of 1850 ± 10 yr BP (Froggatt and Lowe, 1990). However, there are many problems converting this to a calendar date, because the age falls in a period of rapid ^{14}C fluctuation and low curve probability. A calendar date of AD 177 (1 σ range of AD 166-195) has been derived by curve matching of a sequence of ^{14}C ages on tree rings from Pureora buried forest trees (J. G. Palmer, pers. comm. 1988 to Froggatt and Lowe, 1990).

Collection and interpretation of the buried forest data have presented an opportunity to evaluate aspects of the volcanic succession hypothesis of McKelvey (1963, 1986). In a detailed study of the lower altitude indigenous forests of west Taupo, McKelvey (1963) described a zonal and concentric forest pattern about Lake Taupo, and equated successional status to this spatial pattern. Nearest to Lake Taupo and on thick pumice were younger dense mixed podocarp forests, whereas away from the lake, on thin pumice, forests were older and had a substantial component of the broadleaved species tawa and northern rata. He suggested that forests in inner zones, with time, will change to become more similar in composition to those in the outer zones (= convergence) as centripetal (towards Lake Taupo) colonisation proceeds. Thus the volcanic succession hypothesis postulates an initial dominance of podocarps, which then diminish as broadleaved species increase in prominence until, finally, broadleaved species dominate. McKelvey (1963) stated that most lower-altitude types are now being replaced by forest in which tawa will be dominant and which will have a small rimu component. Regeneration trends indicated that tawa was currently aggressively colonising almost all dense podocarp stands, but was slow to enter where pumice was thickest and coarsest and drainage was sometimes impeded.

This study shows that the present day vegetation pattern along a 20 km transect from Pureora to Benneydale is similar to that described by McKelvey (1963), *i.e.* podocarp dominance gives way to broadleaved dominance. However, before the Taupo eruption dense podocarp forest was characteristic of all four sites along the transect, though there were significant compositional differences. Rimu and tanekaha were dominant at the Pureora end, whereas rimu dominated at Thomas, Tocker and Benneydale. In addition, broadleaved species, *e.g.* northern rata, rewarewa, white maire and black maire, were more important westward at the Benneydale end. These spatial differences are also reflected in the sample classification, and there is very little overlap between buried forests despite apparent terrain/drainage overlaps. The forests had all developed virtually undisturbed by volcanic eruption, with only very minor soil rejuvenation, for about 12,000 years (see Clarkson *et al.*, 1988) yet had maintained their differences. We suggest that there had been little or no convergence of the type predicted for present day forests by McKelvey (1963).

Comparisons between the buried and present-day forests are severely limited by the landscape modification induced by man since the Taupo eruption. Large tracts of forest in the central North Island were burned by the Maori (Bidwill, 1952; Fletcher, 1914) and much of the vegetation today still bears the imprint of past firing. For example, in Waipapa mire, 7 km north-west of Pureora buried forest, charred logs of miro, *Phyllocladus* and possibly kahikatea indicate forest once grew at sites now mapped as *Baumea-gleichenia-lepidosperma* fern-sedgeland and *Baumea-lepidosperma* sedgeland by Leathwick (1987). At the Pureora buried forest site, the extant shrub and herbaceous mire vegetation and adjoining forest margin are also fire-derived. The manuka-dominated vegetation covering the Benneydale, Tocker and Thomas buried forest sites at the turn of the century probably resulted from the shifting cultivation techniques practised by the Maori, as there is a long-established Maori settlement at Tiroa, 1 km north-east of the Thomas site, reputed to date back at least 400 years (Kelly, 1949). Landscape modification increased rapidly after the arrival of the European settlers, who cleared areas topographically similar to the buried forest sites for farming and exotic forestry.

Evaluation of the volcanic sucession hypothesis is also hampered by the absence of macrofossil data for periods between *c.* AD 130 and the present day, and more important, before *c.* AD 130. Although the podocarp dominance of the buried forests contradicts the notion that equilibrium is achieved with the broadleaved (mainly tawa) stage (McKelvey, 1986), we do not know whether a broadleaved stage ever existed at the sites in the *c.* 12,000 years between the end of the last glaciation and the Taupo eruption. Pollen analysis of cores from the buried forest sites, notwithstanding off-site pollen 'contamination', may help work out past successions.

McKelvey (1963) and Gibbs (1983) suggested that the present competitiveness of tawa and other broadleaved species in the lower altitude forests is the result of increased soil fertility produced by the weathering of the skeletal pumice. Weathering has been continuous throughout a pedologically short time period of *c.* 1800 years since the Taupo eruption. However, studies by Stevens and Walker (1970), Wardle (1980), Wells (1959) and others, and the evidence of this study, suggest that after a pedologically longer period, such soils become less fertile through leaching, podzolisation, and loss of nutrients. Soils would degrade rapidly on the central North Island pumicelands, due to their thick pumice layer, large particle size, and relatively high rainfall (WC Rijkse, pers. comm., 1987). This study, and the known longevity of podocarps compared with broadleaved trees, indicate that *c.* 1800 years is too short to predict future long-term trends in species composition in west Taupo forests. Although no data which would indisputably confirm or refute McKelvey's volcanic succession hypothesis are available for the central North Island, studies elsewhere, *e.g.*, reviewed in White (1979), show that, although there may be short term convergence of vegetation types, the process slows down; the end result falls short of independence from initial site conditions and topography. Thus, in the short term (hundreds of years), improved soil fertility will result in increased broadleaved species, but in the longer term (thousands of years), soil podzolisation and nutrient loss ensure a re-expansion of certain podocarps. This, in essence, is Gibbs's (1983) evolutionary spiral theory (discussed in detail in Clarkson *et al.*, 1988) and the 14,000 year successional pattern outlined by Wardle (1980).

The first forest around Pureora after the Taupo eruption was dominated by matai and totara, and had established within 450 years (Clarkson *et al.*, 1986). Although podocarps are still prominent in the west Taupo area, there has been an influx of the more fertility-demanding broadleaved species, notably tawa, as the soil has weathered and an organic component added (McKelvey, 1963; Gibbs, 1983). The rate of change depends on local site conditions, topography and climate. For example, forests on flat to undulating land and on thick pumice near the Pureora buried forest site have elements of both the podocarp and broadleaved stages (Clarkson *et al.*, 1988), whereas those on undulating and hilly terrain around Benneydale, where the climate is milder and the pumice deposit thinner, are already well advanced into the broadleaved stage and this stage could be expected to persist longer. Some of the most inhospitable sites, for example, with thick pumice and poor drainage, may never have a true broadleaved stage, and others may have already reached their broadleaved peak. Examples here are probably those within the edaphic L1 subtype, *i.e.*, matai/ miro/ totara-dominated dense mixed podocarps in which tawa is scarce or absent (McKelvey, 1963) and the (rimu)/tawa-quintinia forest type of Leathwick (1987) in Waipapa Ecological Area, in which tawa is in poor health. The current (since 5,000 yr BP) drought- and frost-prone climate (McGlone and Topping, 1977) may also have an important role in determining forest composition, tipping the competitive balance even more away from tawa towards podocarps (see Kelly, 1987). We conclude that, under the present climate regime and in the absence of major disturbance, the less nutrient-demanding podocarp species, such as those that were dominating the buried forest sites prior to the Taupo eruption, should again dominate forest on flat to undulating terrain in the Pureora-Benneydale district.

ACKNOWLEDGEMENTS

This study was funded by a New Zealand Lottery Board grant. Facilities and support were provided by Forest Research Institute, Rotorua, via Dr J.W. Herbert and Botany Division, DSIR, Rotorua and Christchurch via Dr M.S. McGlone. Permission to work on private land was graciously given by Mr M. Murcott, Mr M. Thomas and Mrs R.J. Tocker. Field assistance was provided by Messrs G.R. Dickinson, G.A. Steward, W.B. Shaw, Dr J.W. Herbert and Mr and Mrs W.H. Dickinson. Mr M.I. Dawson cut wood sections for microscope examination, Mr J.R. Leathwick ran the computer programmes and made available unpublished National Forest Survey data, and Mrs C. Pakes typed the manuscript. Mr J.L. Nicholls, Dr G.M. Rogers, Dr M.S. McGlone and Mr J.R. Leathwick commented on earlier drafts of this manuscript.

REFERENCES

Atkinson, I.A.E., 1985. Derivation of vegetation mapping units for an ecological survey of Tongariro National Park North Island, New Zealand. *N.Z. Journal of Botany* 23: 361-78.

Bidwill, J.C., 1952. *Rambles in New Zealand* (reprint). Pegasus Press, Christchurch.

Bussell, M.R., 1988. Modern pollen rain, central North Island, New Zealand. *N.Z. Journal of Botany* 26: 297-315.

Clarkson, B.D., Clarkson, B.R., and McGlone, M., 1986. Vegetation history of some west Taupo mires. *In* B.Veale and J.Innes (comps): *Ecological research in the central North Island volcanic plateau region*, pp. 34-37. Proceedings of a New Zealand Forest Service workshop. Forest Research Institute, Rotorua.

Clarkson, B.R., Patel, R.N., and Clarkson, B.D. 1988. Composition and structure of forest overwhelmed at Pureora, central North Island, New Zealand, during the Taupo eruption (*c.* AD 130). *Journal of the Royal Society of N.Z.* 18: 417-436.

Fletcher, H.J., 1914. Notes on comparatively recent changes in the vegetation of the Taupo District. *Transactions of the N.Z. Institute* 47: 70-72.

Froggatt, P.C., 1981. Stratigraphy and nature of Taupo Pumice Formation. *N.Z. Journal of Geology and Geophysics* 24: 231-248.

Froggatt, P.C., and Lowe, D.J., 1990. A review of late Quaternary silicic and some other tephra formations from New Zealand: their stratigraphy, nomenclature, distribution, volume, and age. *N.Z. Journal of Geology and Geophysics* 33: 89-109.

Gibbs, H.S., 1983. Development and relationships of lowland forest soils. *In* K.Thompson, A.P. Hodder and A.S. Edmonds (Eds): *Lowland Forests of New Zealand*, pp. 35-44. Proceedings of a University of Waikato Symposium: Centre of Continuing Education and Environmental Studies Unit, University of Waikato, Hamilton.

Hay, R.F., 1967. Sheet 7 Taranaki (ed. 1) *Geological map of New Zealand* 1:250 000. Wellington, Department of Scientific and Industrial Research.

Hessell, J.W.D., 1986. The climate of Pureora Forest. *In* B. Veale and J. Innes (comps.): *Ecological research in the central North Island volcanic plateau region*, p. 27. Proceedings of a New Zealand Forest Service Workshop. Forest Research Institute, Rotorua.

Hill, M.O., 1979a. *TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes*. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

———, 1979b. *DECORANA - A FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Section of Ecology and Systematics, Cornell University, Ithaca, New York.

Kelly, D., 1987. Slow recovery of *Beilschmiedia tawa* after severe frosts in Inland Taranaki, New Zealand. *N.Z. Journal of Ecology* 10: 137-140.

Kelly, L.G. 1949. *Tainui: the story of Hoturoa and his descendants*. The Polynesian Society (Inc.), Wellington.

Knowles, B., and Beveridge, A.E. 1982. Biological flora of New Zealand 9. *Beilschmiedia tawa* (A. Cunn.) Benth. et Hook. F. ex Kirk (Lauraceae) Tawa. *N.Z. Journal of Botany* 20: 37-54.

Leathwick, J.R., 1987. Waipapa Ecological Area: A study of vegetation pattern in a scientific reserve. *Forest Research Institute Bulletin* No. 130. Ministry of Forestry, Forest Research Institute, Rotorua.

McGlone, M.S., and Topping, W.W., 1977. Aranuian (post-glacial) pollen diagrams from the Tongariro region, North Island, New Zealand. *N.Z. Journal of Botany* 15: 749-760.

McKelvey, P.J., 1963. The synecology of the West Taupo indigenous forest. *N.Z. Forest Service Bulletin* No. 14.

——— 1986. Future research perspective. *In* B. Veale and J. Innes (comps): *Ecological research in the central North Island volcanic plateau region*, pp. 54-57. Proceedings of a New Zealand Forest Service workshop. Forest Research Institute, Rotorua.

New Zealand Meteorological Service, 1973. Rainfall normals for New Zealand, 1941 to 1970. *N.Z. Meteorological Service Miscellaneous Publication* 145. Wellington, Government Printer.

——— 1985. Climatic map series 1:2 000 000. Part 4: Air temperatures. *N.Z. Meteorological Service Miscellaneous Publication* 175. Wellington, Government Printer.

Pullar, W.A., and Patel, R.N., 1972. Identification of tree stumps and driftwood associated with tephra layers in alluvium, peat and dune sands. *N.Z. Journal of Botany* 10: 605-614.

Rijkse, W.C., and Wilde, R.H., 1976. Soil map of the King Country - Sheet 1. Scale 1:63 360. *N.Z. Soil Bureau Map* 170/1.

Stevens, P.R., and Walker, T.W., 1970. The chronosequence concept and soil formation. *Quarterly Review of Biology* 45: 330-350.

Wardle, P., 1980. Primary succession in Westland National Park and its vicinity, New Zealand. *N.Z. Journal of Botany* 18: 221-232.

Wells, N., 1959. Soil sequences from basalt and greywacke. *Proceedings of the N.Z. Institute of Agricultural Science*: 40-44.

White, P.S., 1979. Pattern, process and natural disturbance in vegetation. *The Botanical Review* 45: 229-299.

Received 26 July 1991; accepted 22 October 1991

© *Journal of the Royal Society of New Zealand,*
Volume 22, Number 2, June 1992, pp 77–90

Late Pleistocene palynology of terrestrial cover beds at the type section of the Rapanui Terrace, Wanganui, New Zealand

M. Royd Bussell*

This study investigates the vegetational and climatic history recorded by fossil pollen preserved in terrestrial cover beds at the type section of the Rapanui Marine Terrace, Wanganui, New Zealand. At this section, laterally extensive Rapanui Lignite and Rapanui Dunesand overlie marine sands of the Rapanui Formation, which were deposited after the cutting of the Rapanui marine platform during the last interglacial *sensu stricto.*

The lowermost sample, below Rapanui Lignite proper, contains a pollen assemblage derived from podocarp-hardwood forest, indicating a palaeoenvironment similar to, or cooler and drier than, the present. The Rapanui Lignite contains pollen assemblages derived from a low forest/shrubland with prominent Myrtaceae, and including a now-extinct *Acacia*-type. These assemblages are derived from vegetation lacking a modern analogue in New Zealand, and they are considered to indicate a palaeoclimate which was also cooler and possibly drier and windier than at present. The presence of *Libocedrus* and *Acacia*-type on the Wanganui lowlands during the period of deposition of Rapanui Lignite indicates important late Pleistocene biogeographic differences for these taxa, compared with the present.

Since the Rapanui Formation marine sands are estimated to be *c.* 120,000 years old, and the overlying terrestrial sediment appears to be more or less conformable, the lowermost pollen sample probably represents the end of the last interglacial (oxygen isotope substage 5e) or the transition period to the following stadial. The Rapanui Lignite is correlated with stadial oxygen isotope substage 5d, and is estimated to date to *c.* 110,000 years ago.

Keywords: pollen, Pleistocene, Rapanui Terrace, Rapanui Lignite, Rapanui Dunesand, Rapanui Formation, marine terraces, oxygen isotopes, vegetation history, climate, palaeoecology, biogeography, Acacia*-type*

INTRODUCTION

The presence of a well preserved suite of upper Pleistocene marine platforms in the south Taranaki-Wanganui district of New Zealand, at 39–45°S latitude and 173°45′–175°E longitude, offers the chance to develop a long record of vegetational and climatic history for the last 600,000 years for this region. Ages have been estimated for the cutting of the marine platforms (Pillans, 1983, 1990) and the terrestrial cover beds of the terraces contain lignites which yield abundant fossil pollen, have a distinctive loess stratigraphy (Pillans, 1988), and contain both andesitic and rhyolitic tephra marker beds, some of which have been independently dated.

A number of long, detailed vegetational and climatic histories have already been documented for different terrace cover bed sequences (*e.g.* McGlone *et al.*, 1984; Pillans *et al.*, 1988; Bussell, 1988a, 1990; Bussell and Pillans, 1992), which provide a discontinuous record of the last *c.* 400,000 yr.

---

* Shell Todd Oil Services Limited, Private Bag, New Plymouth, New Zealand

Table 1 – Nomenclature and ages of south Taranaki-Wanganui marine terraces cut during the last *c.* 350,000 yr (Pillans 1983, 1990).

Terrace	Approx. age (yr)	Correlation with oxygen isotope stage/substage
Rakaupiko	60,000	3
Hauriri	80,000	5a
Inaha	100,000	5c
Rapanui	120,000	5e
Ngarino	210,000	7
Brunswick	310,000	9
Braemore	340,000	9

This paper presents the results of pollen analysis of the cover beds of the Rapanui Terrace, which Pillans (1983) considered to have been cut *c.* 120,000 yr ago during the last interglacial (oxygen isotope substage 5e). The site investigated is the Rapanui Terrace type section (Fleming, 1953) at Castlecliff Beach, Wanganui, New Zealand (latitude 39° 55′ S, longitude 174° 57′ E, at grid reference R22/432754*; Fig. 1). It is located 80km east of the Taranaki Volcanic Centre ringplain and 100km south-southwest of the Taupo Volcanic Zone (Fig. 1).

The site was previously palynologically investigated by W.F. Harris and R.A. Couper. Their results have never been fully published, but were summarised in Fleming (1953). Unfortunately, the summary version combined data from two stratigraphically and geographically separate sites, as further discussed below.

The Rapanui Lignite Site provides a vegetational and climatic history from the end of the last interglacial to the following stadial period (end oxygen isotope substage 5e to substage 5d) that is closely linked with sea level changes. A comparison is made with other published sites from the region.

REGIONAL SETTING

Depositional setting

Table 1 presents the nomenclature and ages of the marine terraces cut during interglacial and interstadial periods of the last *c.* 350,000 yr in the south Taranaki-Wanganui district. The terrace strandlines in the area of the Rapanui Lignite site are mapped in Fig. 1.

The surfaces of the cover beds form a 15km wide coastal terraced landscape that contrasts markedly with the deeply dissected, soft marine sediments of the higher altitude hinterland. Holocene sand-dune complexes are present along the coastal areas, and the terraces are abruptly cliffed northwest of Wanganui except where major rivers intersect the coast.

To the northwest, Mt Taranaki (Egmont) is a 2518m high, presently dormant late Pleistocene andesitic stratovolcano. The present massif is less than 10,000 years old (Neall *et al.*, 1986) but there are older centres of the Taranaki Volcanic Zone northwest of Mt Taranaki, which date back to 1.74 ± 0.03 Myr (Neall, 1979). The local Pleistocene volcanic activity has been largely restricted to pyroclastic deposition on the ringplain, but tephra was at times distributed southeast to the Wanganui district. To the north-northeast, the Taupo Volcanic Zone has been a major centre of rhyolitic and andesitic volcanism in the late Pleistocene, and has sourced important rhyolitic marker tephra in the Taranaki sequence.

---

[*] Grid references and fossil locality numbers are recorded in the N.Z. Fossil Record File and are based on the national thousand metre grid of the 1:50,000 map series, NZMS260

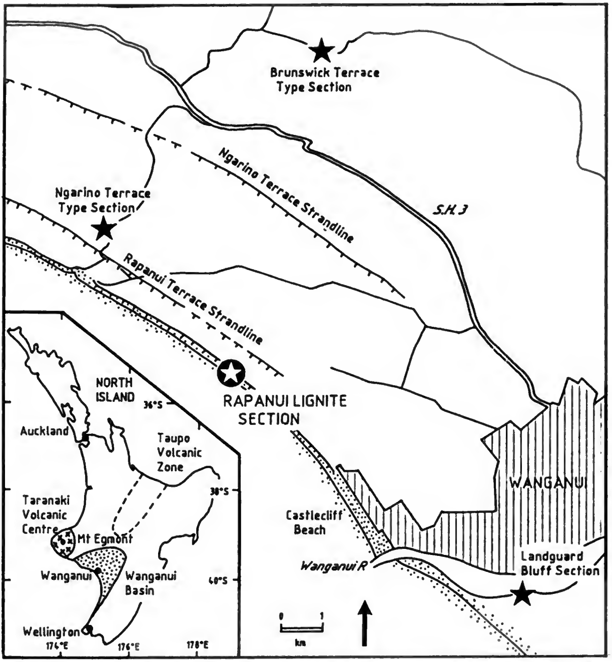


Fig. 1 – Location of the Rapanui Lignite Site in relation to the mapped strandlines of marine terraces (after Pillans, 1990).

Major rivers in the area are thought to have had floodplains which acted as sources for widespread loess deposits while they aggraded terraces during cool-climate phases of the last *c.* 300,000 yr (Milne, 1973).

Climate

Coastal regions, such as Wanganui, currently enjoy a mild, warm-temperate climate with few extremes, while cooler annual average temperatures and higher average rainfall are experienced in hinterland regions, and frosts and fogs may be common. Annual rainfall at Wanganui is 900 mm and is evenly distributed through the year. Mean annual temperature at Wanganui is 13.6°C. West and northwest winds prevail with relatively frequent gales.

Vegetation

Except for small pockets, there is little remaining of the coastal-lowland forests that once covered the south Taranaki-Wanganui district. Present land usage is principally for dairy farming, and rich pasture grows on the freely draining, fertile, yellow-brown earth soils of the terrace surfaces.

The original coastal to semi-coastal forest comprised a low canopy of *Dysoxylum spectabile, Rhopalostylis sapida, Corynocarpus laevigatus, Beilschmiedia tawa, Elaeocarpus dentatus, Alectryon excelsus, Hedycarya arborea,* and *Laurelia novaezelandiae* (Esler, 1978).

Podocarp-hardwood forest dominated by a canopy of *Beilschmiedia tawa* covered lowland areas inland from Wanganui. Podocarps such as *Dacrydium cupressinum, Prumnopitys taxifolia, P. ferruginea, Podocarpus totara,* and *Dacrycarpus dacrydioides* emerged above this canopy, together with the hardwood *Metrosideros robusta*. Poorly drained areas supported dense stands of *D. dacrydioides*.

Further inland, behind the oldest marine terrace remnants, *Nothofagus solandri* var. *solandri* forms ridgeline forests (above *c.* 450m) on the poorer soils. The associated canopy trees are *Weinmannia racemosa* (which altitudinally replaces *Beilschmiedia tawa), Podocarpus hallii* (which altitudinally replaces *P. totara),* and *B. tawa* (Nicholls, 1956).

Clarkson (1985, 1986) described the altitudinal vegetation zones of Egmont National Park, and the vegetation communities of central-western North Island have been briefly described by Bussell (1988b). On Mt Taranaki, where *Nothofagus* is absent, montane podocarp-hardwood forest forms the timberline at *c.* 1050m, replaced at successively higher altitudes by subalpine shrubland, grassland, herbfield, and mossfield. Holocene volcanic activity has strongly affected Mt Taranaki vegetation (Druce, 1966) but the influences of the volcano on vegetation elsewhere have probably been largely confined to the ringplain. Pleistocene volcanic activity in the distant Taupo Volcanic Zone is unlikely to have severely influenced vegetation in south Taranaki-Wanganui except along the valleys of major rivers which have their headwaters in that region.

THE RAPANUI LIGNITE SECTION

Local terrace sequence

The Rapanui Lignite Section at Castlecliff Beach, Wanganui, is a cliff exposure of the Rapanui Terrace marine platform and associated cover beds originally mapped and described by Fleming (1953) as the type locality for the Rapanui Formation. Lensen (1959) regionally mapped the marine terrace sequence at Wanganui, and Dickson *et al.* (1974) differentiated the older Ngarino Terrace from the previously mapped Rapanui. The strandline of the Rapanui Terrace is preserved inland from Castlecliff Beach (Fig. 1). Pillans (1983, 1990) recognised two marine terraces younger than the Rapanui, the Inaha and Hauriri Terraces west of the Rapanui Lignite Section, previously mapped as the Rapanui Terrace. Pillans (1983) assigned an age of *c.* 120,000 yr for the cutting of the Rapanui marine platform.

Pillans (1990) mapped the terrace sequence at 1:100,000 scale and formally described and defined each terrace. In contrast to Fleming's (1953) usage, the Rapanui Formation is restricted to include only the marine cover beds of the Rapanui Terrace that overlie the wave cut platform (the "Rapanui Marine Sand" of Fleming, 1953). The terrestrial cover beds of the Rapanui Terrace are considered here to include the Rapanui Lignite and Rapanui Dunesand, but not the Waipuna Delta Conglomerate or Kaiwhara Alluvium. The Waipuna Delta Conglomerate has been shown by Pillans *et al.* (1988) to be a littoral deposit within the Ngarino Terrace marine cover beds, while the Kaiwhara Alluvium has been retained for describing sediments of many depositional settings at Landguard Bluff (Ngarino Terrace: Pillans *et al.*, 1988).

Stratigraphy (Fig. 2)

The Rapanui Lignite Site exposes some 13 m of cover beds of the Rapanui Terrace in a cliff at the back of Castlecliff Beach (Fig. 2). A marine platform at 29 m a.s.l. (13 m below terrace surface) is unconformably cut into neritic sediments of the Shakespeare Group. The

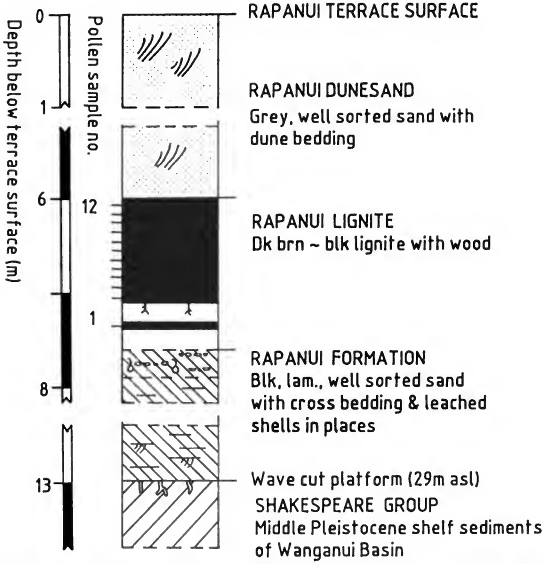

Depth below terrace surface (m)
Pollen sample no.
0
1
6
8
13
12
1
RAPANUI TERRACE SURFACE
RAPANUI DUNESAND
Grey, well sorted sand with dune bedding
RAPANUI LIGNITE
Dk brn ~ blk lignite with wood
RAPANUI FORMATION
Blk, lam., well sorted sand with cross bedding & leached shells in places
Wave cut platform (29m asl)
SHAKESPEARE GROUP
Middle Pleistocene shelf sediments of Wanganui Basin

Fig. 2 – Stratigraphy of the Rapanui Lignite Site (type section of the Rapanui Terrace, Castlecliff Beach, Wanganui).

marine cover beds comprise 5 m of littoral sands with rare leached shells. This is overlain by 0.5 m of sands of probable terrestrial origin, which include a thin lignaceous layer from which the lowermost pollen sample was taken. The Rapanui Lignite overlies and comprises 1.2 m of thick, dark brown lignite; then there is some 6 m of Rapanui Dunesand to the current terrace surface, which has no loess or soil development on it at the pollen site.

Dating

Pillans (1983, 1990) considered the Rapanui marine platform to have been cut at *c.* 120,000 yr ago, that is, during the last interglacial (oxygen isotope substage 5e) marine transgression. This age was calculated using an uplift model for the suite of marine platforms in the region, calibrated with a fission track date on a rhyolitic tephra in the cover beds of an older terrace. The age is also supported by amino acid racemisation dates on Rapanui Lignite, which average *c.* 110,000 yr ago (Pillans, 1990). Furthermore, loess stratigraphy in the region suggests that four loess units overlie the Rapanui Terrace, and the oldest loess ('L4') was considered by Pillans (1988) to be *c.* 100,000–120,000 yr old. Since the Rapanui Lignite closely overlies the marine cover beds in an apparently conformable sequence, and because the site is close to the terrace strandline, then the Rapanui Lignite may be expected to date soon after the time of terrace cutting.

PALYNOLOGY

Methods

Pollen samples were analysed from 10 cm intervals within the Rapanui Lignite, and one sample was analysed from a lower lignaceous horizon (Fig. 2). Sample processing methods follow those of Faegri and Iversen (1975). The sample residues were placed in silicone oil, and slides containing 0.02 ml of suspended sample were prepared and wax-sealed.

A minimum pollen sum of 280 was achieved for all samples. The pollen sum used includes all terrestrial pollen except *Leptospermum*-type and was aimed at providing the clearest information on the extra-local and regional vegetation (Jacobson and Bradshaw, 1981). Bussell (1988a) discusses the choice of this pollen sum in more detail. Charcoal particle areas were also measured for all samples using the method described by Clark (1982).

Interpretation of the pollen assemblages is based partly on modern pollen studies from the region (McGlone, 1982; Bussell, 1988b) and by comparison between the assemblages sampled and those recorded from the Holocene and last glaciation in the area (McIntyre, 1963, 1970; McGlone, 1980; Bussell, 1988c). Norton *et al.* (1986) have shown that selected modern pollen spectra in New Zealand correlate with modern vegetation associations, and that the abundance of certain pollen taxa correlates well with some climatic parameters. Analogues are also made from present day vegetation-climate relationships.

Fig. 3 shows a pollen diagram from the Rapanui Lignite Site. Raw pollen counts for taxa shown in the pollen diagrams and for other taxa not shown are contained in Bussell (1988a). All samples contained abundant, although corroded, pollen.

The pollen diagram

No local pollen zones are designated for this site, although the single sample from the lower thin lignaceous unit does show some important differences.

The lowermost pollen sample from 7.38m (sample 1, Fig. 3) is dominated by the pollen of *Dacrydium cupressinum*; pollen of *Prumnopitys taxifolia* and *Coprosma*, and spores of *Cyathea*, are common.

The two pollen samples from the base of the Rapanui Lignite (samples 2 and 3, Fig. 3) have substantially reduced percentages for gymnosperm tree pollen compared with sample 1, and an unusual assemblage dominated by *Metrosideros*-type pollen at levels up to 83%. Because the pollen was not well preserved, identification of separate taxa within the Myrtaceae was more tentative than usual, and although I felt that much of the pollen present in these and overlying samples was *Metrosideros*, some may be attributable to either *Neomyrtus*-type or, in the case of samples 2 and 3 particularly, the semi-swamp tree *Syzygium maire*.

Pollen samples 4–12 (Fig. 3) have lower amounts of *Metrosideros*-type pollen, and there is general decline of this type upwards through the Rapanui Lignite. *Coprosma* pollen, on the other hand, shows a marked upward increase in abundance, with a maximum of 67%. *Leptospermum*-type pollen also shows upward rise, with a maximum below the top of 130% (it is excluded from the pollen sum). *Libocedrus* pollen is common throughout the Rapanui Lignite, averaging *c.* 5%, and shows a peak of 16% in the uppermost sample (sample 12, Fig. 3). *Nothofagus menziesii* pollen is consistently present at low levels from samples 5–12. Grass pollen is common in the middle of the Rapanui Lignite, but is sparse in other samples. Asteraceae (Tubuliflorae) and *Phyllocladus* pollen are most common in the upper half. *Acacia*-type polyads comprise 1% of the pollen sum in sample 6. Local swamp pollen is sparse in the lower half of the pollen sequence, but sedge, rush and *Phormium* pollen are common in the middle and upper Rapanui Lignite. *Phormium* pollen is abundant (55%) in sample 5, and declines upward. Fern spores are not prolific in this pollen sequence, and spores of *Cyathea*, the most common taxon represented, are most common in the lower half of the pollen sequence. Charcoal particles are present but infrequent throughout the pollen sequence, except in sample 10, where they reach a peak of 33 cm^2/cm^3.

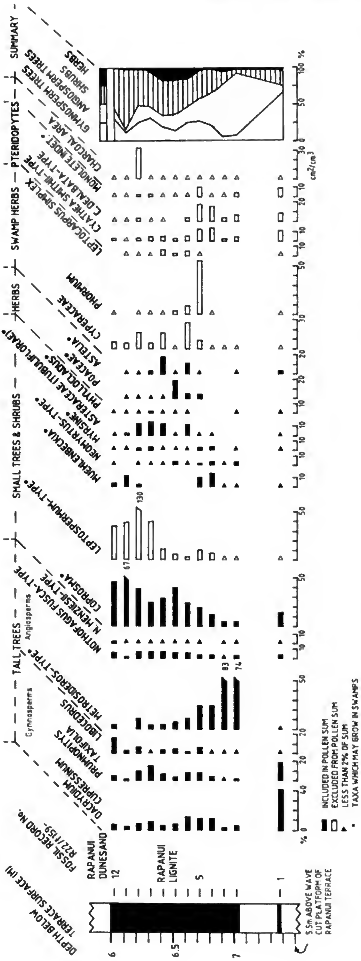


Fig. 3 – Pollen diagram from the Rapanui Lignite Site showing selected taxa. Pollen sum = terrestrial pollen minus *Leptospermum*-type. Numbers 1–12 on the right hand side of the profile show the positions of the samples.

Table 2 – Summary of vegetational and climatic changes recorded at the Rapanui Lignite Site, and their interpretation in terms of climatic stages

Samples	Extra-local vegetation	Climate (compared with present)	Stage	Inferred oxygen isotope substage
Rapanui Lignite (2–12)	Shrubland-low forest with Myrtaceae and *Acacia*-type	Cooler, drier and windier	Stadial	5d
Lowest sample (1)	Podocarp-hardwood forest	Similar, or cooler and drier	End of interglacial or transition to stadial	5e–5d

VEGETATIONAL AND CLIMATIC HISTORY (Table 2)

Local environmental and vegetational history

During an interglacial period of high sea level, the sea cut the Rapanui Terrace marine platform and deposited marine sediment at the site. Following regression, coastal sand-dunes probably formed, and these were forested where stable. A small inter-dune hollow at the site was most likely occupied by forest, as few pollen grains derived from swamp herbs are represented in sample 1 (Fig. 3). Some pollen of the semi-swamp tree *Dacrycarpus dacrydioides* is present, but this species is unlikely to have been dominant. The local and extra-local arboreal communities may have been similar at this time, so *Dacrydium cupressinum* is envisaged as growing on the site. The presence of the aquatic *Myriophyllum* at this time suggests open water conditions, even if only for a brief period, and *D. cupressinum* apparently can tolerate standing in waterlogged soils once a surface layer of humus has formed (Franklin, 1968).

Some time later, a more permanent and more extensive swamp was established, presumably as a result of stabilisation of the site. Because the Rapanui Lignite is laterally continuous, it must represent a very extensive, poorly drained area. The depositional setting is envisaged as a dune-impounded swamp, although the coast need not have been close to the site.

Initially, semi-swamp forest probably grew on the site, because pollen derived from swamp herbs is scarce. One possibility is that the site may have been dominated by the small swamp tree *Syzygium maire*. Later, the local water table rose to allow the establishment of a sedge-*Phormium* community, in which the rush *Leptocarpus similis*, and the herb *Astelia*, were common (samples 5–12, Fig. 3). *Syzygium*, if dominant earlier, became excluded from the swamp at this time. This community indicates the swamp was fertile. No such extensive swamps of this nature have survived on the Taranaki-Wanganui lowlands to the present day. *Lagarostrobos colensoi* probably grew locally.

Dune activity then overwhelmed the site, after which peat was no longer deposited locally.

Extra-local and regional vegetation history

Initially (sample 1, Fig. 3) the site may have been surrounded by podocarp – ?hardwood forest dominated by *Dacrydium cupressinum*, and with common *Prumnopitys taxifolia*. However the hardwood trees appear to be sparsely represented in the pollen record, probably because they are masked by the high local pollen input of podocarp trees growing on the site, so little can be said of the extra-local forest composition. Likewise, the relative proportions of the podocarp trees may be misleadingly represented in the pollen spectrum because of masking by *D. cupressinum*.

During the time of Rapanui Lignite deposition, the record suggests that the forest in the extra-local community was restricted in extent, even allowing for palynological masking by the abundant *Metrosideros*-type representation in samples 2 and 3 (Fig. 3). Shrubland/low forest, principally comprising *Coprosma*, *Leptospermum*-type, *Muehlenbeckia*, *Neomyrtus*-type, *Myrsine*, and probably *Metrosideros*, may have been the dominant extra-local vegetation at the time of deposition of the lower part of the lignite. This vegetation may have been associated with dune country. Further inland, some podocarp – hardwood forest was probably present.

Later (samples 5–7, Fig. 3), it appears that some open areas occupied by grassland were present nearby. One source of grass pollen may have been from the sandbinder *Spinifex hirsutus*, which could have been common if there were sand-dunes present in the area. *Coprosma* became more common in the surrounding shrubland, and the presence of the now extinct *Acacia*-type indicates that this community does not have a present day analogue. Many of the pollen taxa that are prominent at this time have representatives in the modern flora in coastal to semi-coastal sand-dune scrub. The assemblage and stratigraphic setting (associated with dune-sand) is typical of other assemblages from older deposits in which *Acacia*-type has been identified (*e.g.* Mildenhall, 1972, 1975a, 1975b; Bussell and Mildenhall, 1990). *Libocedrus* was apparently common in the extra-local vegetation, as suggested by pollen records of up to 6% of the sum for this palynologically under-represented tree (McGlone, 1982; Bussell, 1988b). It may have formed isolated pockets of forest perhaps on the margins of interdune hollows, as it presently prefers poorly drained sites (Elder, 1965).

During the time represented by the middle and upper Rapanui Lignite, shrubland/low forest remained the dominant extra-local vegetation community, but *Coprosma* and *Leptospermum*-type increased in abundance. Asteraceae (Tubuliflorae) became common. *Acacia*-type may well have still been present, because Australian modern pollen rain studies have shown that *Acacia* pollen is severely under-represented in most samples (Dodson, 1977, 1983). In the regional forests *Nothofagus fusca*-type and *N. menziesii* increased, but they were most probably not present in the Wanganui lowland. The presence of 16% *Libocedrus* pollen in the uppermost sample (12, Fig. 3), indicates that this tree must have been abundant in the extra-local vegetation of that time.

Climatic history

The lowermost pollen sample (1, Fig. 3) is considered to indicate warm, wet conditions, probably not too dissimilar from the present climate of Wanganui if *Dacrydium cupressinum* was dominant in the podocarp – hardwood forest of the region. However, there is an alternative interpretation, which considers *D. cupressinum* as purely local, and in which *Prumnopitys taxifolia* is the extra-local dominant tree of podocarp – hardwood forest; this scenario suggests cooler, drier conditions than the present.

The vegetation recorded in the Rapanui Lignite itself certainly represents a cooler, probably drier climate than present. This is suggested by (1) the scarcity of pollen from podocarp – hardwood forest, even considering the local masking effects of the common pollen types, and also by (2) the presence of 'cool-climate taxa', principally *Libocedrus*, on the Wanganui lowlands. Some shrubland/low forest may have lived among local sand-dunes; however, many taxa associated with recent pre-clearance coastal to semi-coastal forests on dune country (*e.g. Dodonaea viscosa* and *Rhopalostylis sapida*), are apparently absent, and this would be expected if the climate was cooler than now.

The 1% representation of *Acacia*-type polyads suggests this taxon was growing in vegetation near to the site. Mildenhall (1975a) considered *Acacia*-type pollen to indicate dry, cool to mild, coastal environments, as it was found in assemblages also containing scrub and grassland species, and apparently, coastal swamp sedges. I consider that the site examined here was inland from the coast proper at the time the Rapanui Lignite was deposited, because the sea had regressed after cutting the Rapanui Terrace, and the cooler climate (indicated by the restriction of forest and the presence of cool climate taxa) suggests that the sea level was by inference much lower than at the present day. Sea level fell after the last interglacial, from

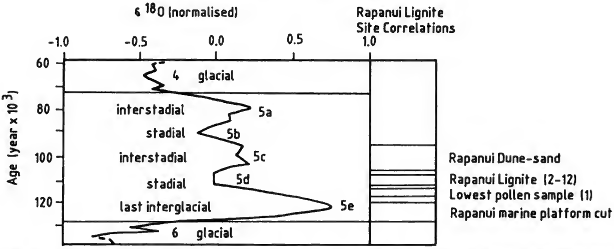


Fig. 4 – Correlation of the Rapanui Lignite Site with the deep sea oxygen isotope record (after Martinson *et al.*, 1987).

+2 m at *c.* 120,000 years ago to –54 m at *c.* 112,000 years ago (Chappell and Shackleton, 1986). Bathymetric data of Lewis and Eade (1974) indicate that a *c.* 50 m sea level fall would produce little change in the palaeogeography of the Wanganui district, but the pollen site would lie some 18 km from the coast at *c.* 112,000 years ago. I consider that the sequence does not contain any important unconformity overlying the marine sediments, and therefore, I infer that the pollen site was most likely part of a lowland plain subject to semi-coastal conditions. I envisage the site as having been subject to frequently cool, dry, possibly windy climatic conditions.

Fire was generally not important in controlling the local to extra-local vegetation, because the charcoal area curve (Fig. 3) shows that there was little charcoal deposition into the site except during the period recorded by sample 10, which records a peak in measured charcoal area.

Although andesitic tephra were reported by Fleming (1953) within Rapanui Lignite, they are not present as prominent horizons in the Lignite at the pollen site, and I do not envisage any influence of volcanism on the vegetation during the time represented by the pollen sequence.

Age and correlation of the Rapanui Lignite site

I consider the lowermost pollen sample to represent the end of the interglacial during which the Rapanui Terrace was cut, because the deposits which this sample came from rest with apparent conformity on the marine deposits of the interglacial, and the pollen assemblage is similar either to the present or to an early post-glacial vegetation of the field area. Thus it is correlated with the end of oxygen isotope substage 5e, or the 5e to 5d transition (Fig. 4). I consider the overlying Rapanui Lignite to represent oxygen isotope substage 5d because, although there may be no exact analogues of some of the communities present at that time, stadial conditions are likely, judging from the pollen assemblages; and the apparently conformable relationship with underlying deposits suggests that the deposits correlate with the stadial immediately following the last interglacial marine transgression. These correlations are shown in Fig. 4 and Table 2. These results tie well with the mean amino acid racemisation dates reported by Pillans (1990) from the Rapanui Lignite.

DISCUSSION

Previous palynological study of Rapanui Lignite

The pollen analytical sequence reported here differs markedly from data reported from the Rapanui Lignite by W.F. Harris and R.A. Couper in Fleming (1953). They reported presence/

absence data for taxa in the Rapanui Lignite, and combined the quantitative results with counts for the same taxa from all samples from the Rapanui Lignite and from the much older Landguard Lignite exposed at Landguard Bluff, Wanganui (Fig. 1). For this reason their data cannot sensibly be compared with the results of this study. Harris and Couper summarised their data by stating that there was "no evidence of marked climatic change during the period of formation" and "the climate was not unlike the present". Their conclusions differ markedly from mine: I consider cooler conditions than present to have prevailed during the Rapanui Lignite deposition. Two possible explanations for the differences are (1) that they sampled the Rapanui Lignite in a different location from this study, and (2) that the lignite is time transgressive. The Castlecliff Beach section is now poorly exposed compared with its condition at the time of Fleming's (1953) field work. Fleming's diagrams of the coastal sections do not indicate any interfingering of separate members of Rapanui Lignite – rather, it is shown as a continuous stratigraphic unit with thickness variations. My field investigations, however, indicate that the Rapanui Lignite is discontinuous along the Castlecliff coastal section, and cannot be assumed to be coeval in all locations. Holocene lignites exposed at Waverley Beach, which were deposited in a setting similar to that of the Rapanui Lignite, have been shown to be diachronous (Bussell, 1988b).

Comparison with nearby sites

Published detailed Pleistocene vegetational histories from the Taranaki-Wanganui district include those of Dickson *et al.* (1974), McGlone *et al.* (1984), Pillans *et al.* (1988), Bussell (1990), and Bussell and Pillans (1992). The pollen spectrum from the lowermost sample at the Rapanui Lignite Site is similar to the interglacial pollen assemblages reported from pollen Zone 3 at the Landguard Bluff Site, Wanganui (Pillans *et al.*, 1988) and from uppermost pollen Zone OH5 at the Ohawe East Site, Hawera (Bussell, 1990). All these assemblages lack common *Ascarina* pollen, distinctive of interglacial maxima in this region (Bussell, 1988a; Bussell and Pillans, 1992). At Landguard Bluff, Zone 3 is correlated with an older interglacial than at the Rapanui Lignite Site. However, it is possible that the upper pollen zone OH5 at Ohawe East could be broadly contemporaneous with the lower pollen sample at the Rapanui Lignite Site (late oxygen isotope substage 5e).

None of the above published studies report pollen assemblages similar to those I found in the Rapanui Lignite. The distinctive features of Myrtaceae pollen dominance with common *Libocedrus* and sporadic *Acacia*-type pollen is not typical of older Tertiary pollen assemblages either[1], and has no modern analogue in New Zealand vegetation.

The Rapanui Lignite may also be partially contemporaneous with strata exposed in a site on the Waikanae River, 105 km south of Wanganui (Fleming, 1972; Mildenhall, 1973). Samples analysed from the Waimahoe Lignite, which overlies last interglacial Otaki Dunesand, contain similar pollen assemblages to those in Rapanui Lignite. The Waimahoe Lignite analyses have never been fully published, which prevents a detailed comparison at present.

Biogeography

The Rapanui Lignite contains some pollen types sourced from taxa that are now either extinct in New Zealand, not present in south Taranaki-Wanganui, or are present in Taranaki but grow at higher altitude locations.

Three *Acacia*-type polyads are present in sample 6. Since this taxon is typically severely under-represented in modern pollen rain in Australia (Dodson, 1977, 1983), the implication for the Rapanui Site is that the source plants were growing locally at the time represented by sample 6. *Acacia*-type pollen-producing taxa are now extinct in New Zealand, yet, as more fully discussed by Bussell and Mildenhall (1990), these results indicate that *Acacia*-type plants were present in the late Pleistocene in Wanganui district. The Rapanui Lignite Site provides the youngest known occurrence of *Acacia*-type pollen in New Zealand.

---

[1] Assemblages reported by Mildenhall (1975a,b) are similar but lack common *Libocedrus* pollen.

The presence of common *Libocedrus* on the Wanganui lowlands during the deposition of the Rapanui Lignite indicates a substantial difference in the late Pleistocene biogeographic range of this taxon compared with today. At present, *Libocedrus bidwillii* grows mainly in upper montane forest on Mt Taranaki (Egmont) in western Taranaki, in the Ruahine Ranges 90 km east of Wanganui, and on the central North Island volcanic mountains. Without macrofossil evidence it is difficult certainly to exclude the possibility that the pollen encountered may be derived from the small tree *L. plumosa*, which is now absent from south Taranaki-Wanganui but grows in lowland forest in northwest Nelson (South Island) and north of around latitude 38°S in North Island. However, given the associated pollen assemblages for *Libocedrus*, it seems more reasonable to assume that the pollen is derived from *L. bidwillii*.

Nothofagus menziesii, Lagarostrobos colensoi, and *Phyllocladus* pollen are present at levels up to 2% in Rapanui Lignite. None of these taxa now live in south Taranaki-Wanganui, but were present in the area in the late Pleistocene during times of cooler climate than present (McGlone, 1980; McGlone *et al.*, 1984; Pillans *et al.*, 1988; Bussell, 1988a, 1990). The low levels recorded in this study should not be taken to confirm their certain presence in the Wanganui lowlands during the time of deposition of Rapanui Lignite, since long distance dispersal of some of these pollen types cannot be ruled out (Macphail and McQueen, 1983).

The examples given above, for *Libocedrus* and *Acacia*-type in particular, indicate significant differences in Pleistocene biogeography in south Taranaki-Wanganui compared with the present. Further details of the ancient vegetation at the Rapanui Lignite Site and elsewhere are hidden by our present inability to resolve the identification of many pollen types beyond the generic level.

CONCLUSIONS

1. The Rapanui Lignite Site contains pollen assemblages derived from "late interglacial" podocarp-hardwood forest and stadial low forest/shrubland. The climate is inferred to have been initially similar to, or slightly cooler and drier than at present, then much cooler and possibly drier and windier than at present during Rapanui Lignite deposition.
2. The lowermost pollen sample is correlated with late last interglacial oxygen isotope substage 5e or the following transition period to stadial oxygen isotope substage 5d, which is represented by Rapanui Lignite, considered to be *c.* 110,000 years old.
3. Pollen assemblages in Rapanui Lignite are derived from vegetation that has no modern equivalent in New Zealand, and which included the now extinct *Acacia*-type.
4. There have been considerable changes in the late Pleistocene ranges of some taxa in south Taranaki-Wanganui compared with the present.

ACKNOWLEDGEMENTS

Professor J. Chappell, Dr. G. Singh, Dr. B. Pillans, and D. Mildenhall are thanked for advice and review of this study. D. Clark and M. Milne kindly typed the manuscript.

REFERENCES

Bussell, M. R., 1988a. *Quaternary vegetational and climatic changes recorded in cover beds of the South Wanganui Basin marine terraces, New Zealand.* Unpublished Ph.D. dissertation, The Australian National University, Canberra.

——— 1988b. Modern pollen rain, central-western North Island, New Zealand. *N.Z. Journal of Botany* 26: 297–315.

——— 1988c. Mid and late Holocene pollen diagrams and Polynesian deforestation, Wanganui district, New Zealand. *N.Z. Journal of Botany* 26: 431–451.

——— 1990. Palynology of oxygen isotope stage 6 and substage 5e from the cover beds of a marine terrace, Taranaki, New Zealand. *Quaternary Research* 34: 86–100.

Bussell, M. R. and Mildenhall, D. C., 1990. Extinct palynomorphs from middle and late Pleistocene terrestrial sediments, South Wanganui Basin, New Zealand. *N.Z. Journal of Geology and Geophysics* 33: 439–448.

Bussell, M. R. and Pillans, B. J., 1992. Vegetational and climatic history during oxygen isotope stage 9, Wanganui district, New Zealand, and correlation of the Fordell Ash. *Journal of the Royal Society of N.Z.* 22: 41–60.

Chappell, J. and Shackleton, N. J., 1986. Oxygen isotopes and sea level. *Nature* 324: 137–140.

Clark, R. L., 1982. Point count estimation of charcoal in pollen preparations and thin sections of sediments. *Pollen et Spores* 24: 523–535.

Clarkson, B. D., 1985. The vegetation of the Kaitake Range, Egmont National Park, New Zealand. *N.Z. Journal of Botany* 23: 15–31.

——— 1986. Vegetation of Egmont National Park, New Zealand. *National Park Scientific Series* 5.

Dickson, M., Fleming, C. A., and Grant-Taylor, T. L., 1974. Ngarino Terrace: an addition to the late Pleistocene standard sequence in the Wanganui-Taranaki district. *N.Z. Journal of Geology and Geophysics* 17: 789–98.

Dodson, J. R., 1977. Pollen deposition in a small closed drainage basin lake. *Review of Palaeobotany and Palynology* 24: 179–193.

——— 1983. Modern pollen rain in southeastern New South Wales, Australia. *Review of Palaeobotany and Palynology* 38: 249–268.

Druce, A. P., 1966. Tree-ring dating of recent volcanic ash and lapilli, Mt Egmont. *N.Z. Journal of Botany* 4: 3–41.

Elder, N. L., 1965. Vegetation of the Ruahine Range: an introduction. *Transactions of the Royal Society of N.Z.* 3: 13–66.

Esler, A. E., 1978. *Botany of the Manawatu*. New Zealand Department of Scientific and Industrial Research Information Series 127.

Faegri, K. and Iversen, J., 1975. *Textbook of pollen analysis, 3rd ed.*. Blackwell, London.

Fleming, C. A., 1953. The geology of Wanganui Subdivision. *N.Z. Geological Survey Bulletin* 52.

——— 1972. The contribution of ^{14}C dates to the Quaternary geology of the 'Golden Coast', western Wellington. *Tuatara* 19: 61–69.

Franklin, D. A., 1968. Biological flora of New Zealand. 3. *Dacrydium cupressinum* Lamb. (Podocarpaceae) rimu. *N.Z. Journal of Botany* 6: 493–513.

Jacobson, G. L. and Bradshaw, R. H. W., 1981. The selection of sites for paleovegetational studies. *Quaternary Research* 16: 80–96.

Lensen, G. J., 1959. Sheet 10 – Wanganui. *Geological map of New Zealand 1:250,000.* Department of Scientific and Industrial Research, Wellington.

Lewis, K. B. and Eade, J. V., 1974 Sedimentation in the vicinity of the Maui Gas Field. *N.Z. Oceanographic Institute Oceanographic Summary* 6.

McGlone, M. S., 1980. *Late Quaternary vegetation history of central North Island, New Zealand.* Unpublished Ph.D. dissertation, University of Canterbury, Christchurch.

——— 1982. Modern pollen rain, Egmont National Park, New Zealand. *N.Z. Journal of Botany* 20: 253–262.

McGlone, M. S., Neall, V. E., and Pillans, B. J., 1984. Inaha Terrace deposits: a late Quaternary terrestrial record in south Taranaki, New Zealand. *N.Z. Journal of Geology and Geophysics* 27: 35–49

McIntyre, D. J., 1963. Pollen analysis of a peat in Koputaroa Dunesand. Appendix *in* Cowie, J. D. Dune-building phases in the Manawatu district, New Zealand. *N.Z. Journal of Geology and Geophysics* 6: 268–80.

——— 1970. Pollen analysis in the Lindale section, Paraparaumu. Appendix *in* Fleming, C.A. Radiocarbon dating and pollen analyses from Otiran periglacial fans in western Wellington. *Transactions of the Royal Society of N.Z. (Earth Sciences)* 7: 197–208.

Macphail, M. K. and McQueen, D. R., 1983. The value of New Zealand pollen and spores as indicators of Cenozoic vegetation and climates. *Tuatara* 26: 37–59.

Martinson, D. G., Pisias, N. G., Hays, J. D., Imbrie, J., Moore, T. C. Jr, and Shackleton, N. J., 1987. Age dating and the orbital theory of the ice ages: development of a high resolution 0–300,000-year chronostratigraphy. *Quaternary Research* 27: 1–29.

Mildenhall, D. C., 1972. Fossil pollen of *Acacia* type from New Zealand. *N.Z. Journal of Botany* 10: 485–94.

———— 1973. Problem of interpretation of two pollen diagrams from an Otiran (uppermost Pleistocene) section near Waikanae. *In*: Te Punga, M. T.; Mildenhall, D. C. (eds) IX INQUA *Congress guidebook for excursion A13, western North Island,* Pp 134–136.

———— 1975a. Palynology of the *Acacia*-bearing beds in the Komako District, Pohanginia Valley, North Island, New Zealand. *N.Z. Journal of Geology and Geophysics* 18: 209–28.

———— 1975b. Lower Pleistocene palynomorphs from the Ohuka carbonaceous sandstone, southwest Auckland, New Zealand. *N.Z. Journal of Geology and Geophysics* 18: 675–81.

Milne, J. D. G., 1973. Maps and sections of river terraces in the Rangitikei Basin, North Island, New Zealand. 4 sheets, *N.Z. Soil Survey Report* 4.

Neall, V. E., 1979. Sheets P19, P20, and P21. New Plymouth, Egmont, and Manaia (1st ed.), *Geological map of New Zealand 1:50,000*. Three maps and notes (36p). New Zealand Department of Scientific and Industrial Research, Wellington.

Neall, V. E., Stewart, R. B., and Smith, I. E. M., 1986. History and petrology of the Taranaki volcanoes. *In Late Cenozoic volcanism in N.Z. Royal Society of New Zealand Bulletin* 23: 251–263.

Nicholls, J. C., 1956. The historical ecology of the indigenous forest of the Taranaki upland. *N.Z. Journal of Forestry* 7:17–34.

Norton, D. A., McGlone, M. S., and Wigley, T. M. L., 1986. Quantitative analyses of modern pollen – climate relations in New Zealand indigenous forests. *N.Z. Journal of Botany* 24: 331–342.

Pillans, B. J., 1983. Upper Quaternary marine terrace chronology and deformation, south Taranaki, New Zealand. *Geology* 11: 292–297.

———— 1988. Loess chronology in Wanganui Basin, New Zealand. *Proceedings of the International Symposium on Loess, Palmerston North.*

———— 1990. Late Quaternary marine terraces, South Taranaki – Wanganui. *N.Z. Geological Survey Miscellaneous Series Map* 18.

Pillans, B. J., Holgate, G., and McGlone, M., 1988. Climate and sea level during oxygen isotope stage 7b: on land evidence from New Zealand. *Quaternary Research* 29: 176–185.

Received 26 July 1991; accepted 19 November 1991

© Journal of the Royal Society of New Zealand, Volume 22, Number 2, June 1992, pp 91–106

The ecology of a New Zealand grassland lizard guild

G.B. Patterson*

Home ranges and aggressive behaviour, habitat preference and diet were studied in a guild of three congeneric skinks, *Leiolopisma inconspicuum*, *L. maccanni* and *L. nigriplantare polychroma* in tussock grassland in New Zealand. The three species displayed niche differences in microhabitat, prey size and prey taxa; there was extensive overlap along the prey niche axes, but significant differences in microhabitat utilization between species pairs. Interspecific aggression related to specific site defence was observed on numerous occasions. These results suggest that this lizard guild is structured mainly by species-specific microenvironmental preferences, controlled by interspecific competition for space.

Keywords: guild, Leiolopisma nigriplantare polychroma, Leiolopisma inconspicuum, Leiolopisma maccanni, *competition, home range, habitat preference, lizard, grassland, New Zealand*

INTRODUCTION

The idea that similar species cannot coexist has a long, controversial history in ecology (British Ecological Society, 1944; Gilbert *et al*., 1952; Miller, 1967; Vadas, 1990). However, although mechanisms for coexistence that do not rely on ecological differences have been proposed (Silvertown and Law, 1987), on closer examination these still support the idea that most species must be sufficiently ecologically distinct to coexist stably (Chesson, 1991).

In New Zealand, a long-isolated and diverse lizard fauna has evolved, which in some areas comprises unusually large congeneric guilds (Towns *et al*., 1985). Root (1967) defined a guild as a species group that uses the same resource in the same way. The following study describes an investigation of ecology, resource use and morphology in a guild of three cryptic skink species which have only recently been described (Patterson and Daugherty, 1990). *Leiolopisma nigriplantare polychroma*, *L. inconspicuum* and *L. maccanni* are common throughout much of the South Island of New Zealand, although all three are sympatric at very few locations. Although almost identical in appearance, they can be distinguished by colour pattern, particularly in sites where they co-exist (see Discussion). Analysis of allozyme variation unequivocally demonstrates that the species are distinct and are valid over their entire ranges (Daugherty *et al*., 1990).

There are few lizard species anywhere that show greater morphological similarity (until 1990 they were classified as a single subspecies), and so the problem of avoiding competitive exclusion where they are sympatric should be particularly acute. Lizards generally partition resources with respect to when they are active, where they forage and what they eat (Pianka, 1973). I therefore recorded data on activity times and food and habitat utilization for all three species at a locality where they were all present in large numbers. Secondly, the role of competition in structuring the guild was investigated. Although the potential of interspecific competition as a structuring force in natural communities is widely recognized, proof of its prevalence in the wild is largely circumstantial. The unequivocal demonstration of competition under field conditions is fraught with difficulties associated with experimental design and

---

* E.L. Hellaby Grasslands Research Fellow, Department of Conservation, P.O. Box 10–420, Wellington, New Zealand.

data analysis (Hairston, 1989; Jaeger and Walls, 1989). Frequently it is possible only to speculate on the mechanisms underlying the interactions between competing species. Field experiments have the potential to provide direct observations of competition. Such observations were accordingly another aim of this study.

MATERIALS AND METHODS

The study area

The study area (Fig. 1) covered approximately 140km^2 on the southern end of the Rock and Pillar Range and the northern end of the Lammermoor Range in Central Otago, South Island, New Zealand (170° E Long, 45° S Lat). The altitude in this area ranges from 900m to 1070m a.s.l., and the landscape comprises rolling tussock-covered slopes that rise to ridges studded with schist outcrops. The dominant plant in most areas was *Chionochloa rigida* Zotov, the narrow-leaved snow-tussock. Red tussock, *C. rubra* Zotov was dominant in damp areas such as the bottoms of gullies, and *Aciphylla aurea* Oliver, the "golden spaniard", a spiny member of the Umbelliferae, was locally abundant as a co-dominant. Apart from *A. aurea*, the inter-tussock vegetation consisted mainly of the herb *Hypochaeris radicata* L., the low shrubs *Cyathodes fraseri* Allan, *Gaultheria depressa* Hook, *Pernettya macrostigma* Col. and *Pentachondra pumila* R. Br., and the grasses *Anthoxanthum odoratum* L. and *Poa colensoi* Hook. This high-altitude snow tussock grassland has persisted only in areas of New Zealand seldom disturbed by fire and intensive grazing (Mark, 1965).

Sheep and cattle grazed the study area, but not intensively. Other introduced mammals observed in this area during the study were mice (*Mus musculus* L.), rabbits (*Oryctolagus cuniculus* (L.)), hedgehogs (*Erinaceus europaeus* L.), cats (*Felis catus* L.), possums (*Trichosurus vulpecula* (Kerr)), pigs (*Sus scrofa* L.), hares (*Lepus europaeus* Pallas) and ferrets (*Mustela putorius* L.). Mice, cats, ferrets and hawks (*Circus approximans* Peale) are the only lizard predators known to be present.

The winter climate in this region is severe, characterised by hard frosts and heavy snow falls. The mean air temperature at a site at 1000m a.s.l. on the northern end of the Rock and Pillar Range from March 1977 to February 1979 was 5.5°C (Holdsworth, 1981). The summer climate is generally more benign, although it snowed in the study area in December 1982.

Lizards were collected in two ways throughout the 140km^2 study area. They were either caught in traps at 37 sites, each ranging in size from approximately 16m^2 to 3000m^2, or by hand, during the three years from 13 April 1981 to 12 February 1984 (Fig. 1). The trap sites contained from five to 49 pitfall traps, which were laid out for at least four consecutive weeks. Two types of pitfall trap were employed. The first was a plastic container, 9cm across the open end and 11cm deep, which was buried with the top flush with the soil surface. Either the trap contained 10% picric acid or 10% formalin, which killed the skinks within 24 hours, or else holes were punched in the bottom so that rain water could drain out, and a handful of soil was thrown in to attract live lizards for home range determination (*cf* Barwick, 1959). The second type of trap was a 12cm length of 3.5 cm diameter PVC pipe buried upright in the ground with one end flush with the surface. The open base allowed water to drain away, except during exceptionally heavy rain.

Home ranges

I use the term "home range" to mean "that area traversed by the individual in its normal activities of food gathering and mating" (*sensu* Burt, 1943). This definition has the advantages of being simple and biologically meaningful. A territory is regarded as an area defended against other individuals of the same species (Odum and Kuenzler, 1955).

I conducted pitfall trapping to delineate home ranges at three sites within a 100m radius in the study area. I assumed that home ranges were similar in the rest of the 140km^2 study area. Trapping was carried out continuously from 31 January 1982 to 2 May 1982, and 28 September 1982 to 25 April 1983 at sites 1 and 3, and from 28 September 1982 to 25 April

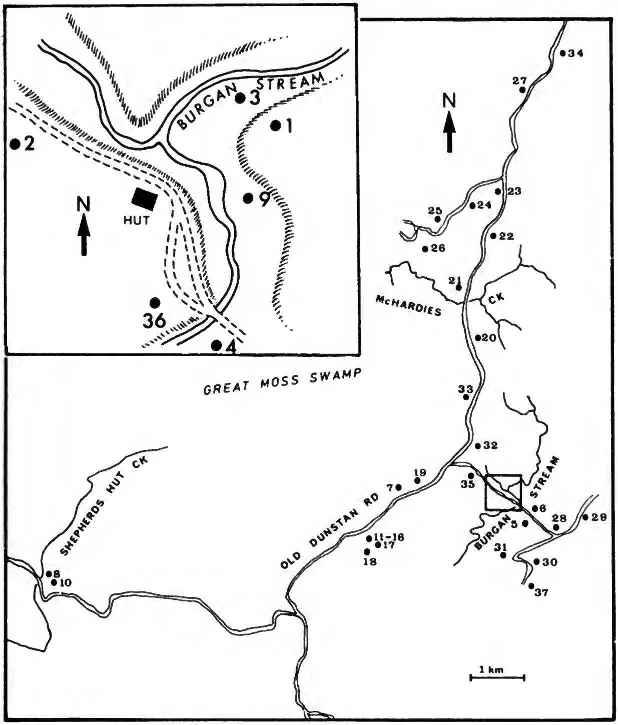


Fig. 1 – Map of pitfall trap sites within the study area.

1983 only at site 2. The relative densities of the dominant plants in the three areas are given below. The figure in brackets is from the cover-abundance index proposed by Braun-Blanquet (1932). Site 3 had 50–75% tussock (4) and at least 5% spaniard (2); site 1 had 25–50% tussock (3) and less than 5% spaniard (+); site 2 had 50–75% tussock (4) and at least 5% spaniard (2). All traps had open tops and were marked with numbered wooden stakes driven into the ground beside them. The traps were placed at intervals of approximately 1m.

Skinks were marked by the usual method of toe-clipping. No more than two toes were removed from an individual. Each skink was toe-clipped upon removal from a trap and the snout-vent (s-v) length and species were recorded, together with the condition of the tail (degree of completeness). The trap number was noted, and the skink released on the ground next to the point of capture.

Behaviour

Because of the difficulty of observing skinks in the wild, I made behavioural observations on captive skinks from October 1983 to April 1984. Skinks from each of the three species were placed inside two 2.3m × 1.0m × 0.4m enclosures within a greenhouse, so that at any one time each enclosure contained nine or fewer skinks. Each enclosure contained a 15cm deep layer of topsoil from the study area, supporting the usual inter-tussock vegetation plus two pitfall traps placed one at each end, a spaniard and a snow tussock. The tussock in one enclosure was 35cm in diameter, and the spaniard was 48cm in diameter. The tussock in the other enclosure was 25cm in diameter, while the spaniard was 42cm in diameter.

Activity patterns and habitat preferences

The activity rhythms of the skinks were examined because subtle temporal differences in daily activity patterns are widespread among lizards, both within and between species (Pianka, 1973).

To measure these patterns, pitfall traps were left in the ground in the study area for 24 hour periods on the following dates: 5–6 March (1230–1230) 1982, 28–29 September (0700–0700) 1982, 29–30 September (0700–0700) 1982, 9–10 October (0800–0800) 1982, 15–16 February (0700–0700) 1983, and 21–22 March (0800–0800) 1983. The traps were checked at every hour, and captured skinks recorded and released.

This information was supplemented by 24-hour observations of the three species in the greenhouse at various times between 25 June and 15 November 1982, and between 20 April and 24 September 1983.

To quantify the distribution of the three species in different microhabitats, the following four microhabitat categories were employed: (1) grasses, (2) herbs and shrubs, (3) rocks resting on soil (henceforward referred to just as "rocks"), and (4) rocks resting on other rocks (henceforward referred to as "rock outcrops"). During February 1983, whenever a skink was sighted in the study area, the species was determined and a description of the immediate microhabitat noted. The microhabitat of skinks that fled from me was recorded from the place of first observation.

Usually a skink's microhabitat was determined without difficulty, but those that were captured in overlapping habitat types were recorded in both microhabitat categories (Marcellini and Mackey, 1970). Each animal was counted only once. Chi-squared tests of independence were used to determine whether interspecific differences in habitat utilization were significant.

Feeding ecology

The food habits of 210 *L. n. polychroma*, 81 *L. inconspicuum* and 110 *L. maccanni* individuals were analysed. Most of the skinks (90%) were collected from preservative-filled pitfall traps, plus some by hand (approximately 10%), from 10 October 1980 to 13 April 1981, 19 October 1981 to 21 April 1982 and 17 September 1982 to 8 June 1983. The animals caught by hand were killed with ether and preserved in 10% picric acid or 10% formalin. All specimens were then placed in 70% ethanol.

Only prey items dissected from the stomach were used in the following analysis, because these were generally intact and easily identifiable. Examining such items in the stomach rather than further along the alimentary canal also avoids bias in the prey data towards hard-bodied arthropods, which leave more recognisable fragments than soft-bodied ones, and may move through the gut at a rate that depends on size (Andrews, 1971).

Stomach contents were measured under a dissecting microscope fitted with an ocular micrometer with 0.1mm gradations. Prey items from the 401 skinks analysed were identified to family level where possible. A few (< 0.5%) of the items were too fragmentary to be identified. Prey size was calculated using the method of Fraser (1976), who assumed that prey items were cylindrical. Since most prey items are not exactly this shape, this means that the contribution by volume of spherical prey such as seeds is underestimated compared with more cylindrical items such as worms.

Skinks used in the prey analysis were divided into three categories for each species: adult males, adult females and subadults. "Subadults" were defined as those individuals of a given species with a s-v length less than the minimum s-v length of sexually mature females in the same species (40.5mm for *L. n. polychroma*, 49.0mm for *L. inconspicuum* and 52.0mm for *L. maccanni*). "Adult males" and "adult females" were likewise defined as those individuals of a given species with s-v lengths greater than or equal to the minimum s-v length of sexually mature females in the same species. Males were assumed to become sexually mature at the same s-v length as females (see Barwick, 1959).

The SPSS program, KOLMOGOROV-SMIRNOV (Nie and Hull, 1981) was used to test prey size differences. The two-tailed Kolmogorov-Smirnov (K-S) test was used on data from *L. n. polychroma* collected from areas where they were syntopic with either *L. inconspicuum* or *L. maccanni*, to see if there were any significant differences in prey size distributions between the populations. The various sex and age classes were tested for significant differences in prey size distributions using the K-S one-tailed test. Differences in head size among the skink size classes were tested with the SPSS program, MANN-WHITNEY U (Nie and Hull, 1981). Interspecific differences in food habits were tested by comparing the stomach contents of skinks caught in pitfall traps or by hand at six different times of the year. The six sample periods were: 1–15 October 1981, 18–29 September 1982, 16–31 October 1982, 1–14 December 1982, 1–14 January 1983, 17–25 April 1983. At least three individuals of each species were caught during each period with prey items in their stomachs. Differences in diet caused by fluctuating seasonal abundances of prey families were minimised by comparing only skinks caught at similar times of the year.

The Mantel test (Mantel, 1967) was used to determine the significance levels of dietary differences among the three species (Patterson, 1986). This test indicates whether prey taxa overlap values were significantly greater within or between species. The Mantel test is useful for comparing prey-taxa data, because it allows the use of variables which are not independent, such as prey-taxa overlap values. Prey items identified to the familial level were used in the test, except for the following groups: larval lepidopterans, adult lepidopterans, dipterans, centipedes, millipedes, berries, collembolans, orthopterans, harvestmen and pseudoscorpions. Each of these groups was classed as a single "morphospecies" because its members, possessing similar behavioural and physical characteristics, probably appear similar to the skinks. Also, grouping many families together in this manner produced the statistically desirable result of eliminating many zero values from the Mantel test.

The head lengths of 267 randomly selected skinks were measured from the posterior end of the interparietal scale to the tip of the snout. The head width, from the lateral edge of the left parietal to the lateral edge of the right, was also measured. Both measurements were taken at 10× magnification under a dissecting microscope fitted with an ocular micrometer with 0.1mm gradations.

To determine the degree of fluctuation in prey families during the year, five invertebrate population estimates were calculated between November 1982 and April 1983 (the "census period") from vacuum samples (see below). Estimates were made on 18 November 1982, 1 December 1982 and 15–16 December 1982 (first estimate); 1–3 January 1983 (second estimate); 29 January 1983, 2–3 February 1983 and 12–14 February 1983 (third estimate); 26–27 February 1983 (fourth estimate); 20 March 1983 and 3–4 April 1983 (fifth estimate). The vacuum samples had to be taken over different time intervals because of the extremely changeable weather in the study area. It was desirable that sampling be carried out in quite uniform climatic conditions, and long intervals between samples were often needed to achieve these.

Thirty two invertebrate census sites of $324m^2$ were located at random within a $0.25km^2$ subsection of the study area. Six sites were sampled to obtain each of the five invertebrate population estimates. No site was sampled in consecutive estimates.

RESULTS

Distribution and home ranges

The distributions of the skink species appeared to be markedly non-random within the study area. All three species were trapped in only two of the 37 trap sites (Table 1), whereas 16 sites collected only one species. The most common species was *L. n. polychroma*, present in all but one site, while the least common was *L. maccanni*, in seven sites. No sites caught no lizards. There was considerable overlap in the home ranges of all three species. During the second period (18–29 September 1982) six animals were recaptured after winter within 10m of one of their capture sites recorded in the previous summer.

Individuals of each species often displayed obvious inter- and intraspecific aggression in the field and in the greenhouse. Many animals were marked by scars from aggressive encounters. This behaviour seemed to be associated with the defence of a specific area within the home range, and consisted mainly of chasing and biting. The defended areas were often basking sites, which were chosen according to the sun's movement during the day. Occasionally, however, defensive aggression appeared to be associated with particular environmental features such as rocks and plants.

In the greenhouse a record was kept of aggressive encounters among the three species concurrently with the pitfall trapping experiment. The skinks were observed at various times of the day, between 0800 and 1700, on most of the days when they were active. Aggressive encounters involved one or more of the following actions between two animals: head-butting, chasing, biting and tail-lashing (the latter usually only in the animal under attack). Such encounters lasted about 5–30 seconds, and at least one encounter was seen on 26 days during the observation period. Fifty eight encounters were observed in total, involving 11 *L. n. polychroma*, eight *L. inconspicuum* and 10 *L. maccanni* individuals. No skink was seen to chase another out of the tussocks, but in 5/21 encounters when *L. maccanni* was the aggressor, the other skink was chased out of an *Aciphylla* plant; the same was seen 5/20 times when *L. inconspicuum* was the aggressor. None of the 17 aggressive encounters involving *L. n. polychroma* as the aggressor were sited in the spaniards.

Table 1 – Distribution of the three species within the study area (1 = *L. n. polychroma*. 2 = *L. inconspicuum*. 3 = *L. maccanni*.

Site no.	Species present	Area (m^2)	Trapping period (weeks)	Date
1	1, 2, 3	450	40	4/82–1/83
2	1,2	300	23	11/82–4/83
3	1,3	330	40	1–10/82
4	1,3	110	23	11/82–4/83
5	1	594	12	3–5/82
6	1	3130	8	2–3/82
7	1,2	540	13	2–5/82
8	1,3	16	12	9–12/81
9	1,3	430	28	1–7/82
10	1,2	16	8	11–12/81
11-16	1,2	324	4	1–2/83
17	2	324	4	1–2/83
18	1,2,3	324	4	1–2/83
19-31	1	–*	16	10/83–2/84
32-36	1,2	–*	16	10/83–2/84
37	1,3	–*	16	10/83–2/84

* Traps were in a straight line

Habitat preference

The sites at which *L. n. polychroma* was the sole species caught (nos 5,6,19–31: Table 1) were quite different structurally from the site (no. 17) at which only *L. inconspicuum* was caught. For example, during the three-month period in 1982 that pitfalls were at site 5, only *L. n. polychroma* (26 individuals) was caught. The density of shrubs in this area was less than 10% (2 on the Braun-Blanquet index), and the tussock density was 75–100% (5 on the Braun-Blanquet index). By contrast, the relative densities of shrubs and tussocks at site 17 were 75–100% and 25–50% respectively (5 and 3 on the index proposed by Braun-Blanquet). A schist outcrop within 100m of one *L. n. polychroma* site was examined regularly over three years. The only species found on or beneath the rocks during these years was *L. maccanni*, although pitfall traps placed in the vicinity caught both *L. n. polychroma* and *L. maccanni*. Presumably *L. n. polychroma* lived in the shrubs and grasses growing between the rocks, while *L. maccanni* lived on or under the rocks, and *L. inconspicuum* lived away from the outcrop altogether.

Not surprisingly, the three species displayed significant differences in microhabitat preferences. Numbers (and percentages) of skinks seen in various microhabitats within the study area are shown in Table 2. There is a significant difference in microhabitat utilization between *L. maccanni* and *L. n. polychroma* ($\chi^2 = 62.9$, d.f.=3, $p<0.001$); *L. n. polychroma* and *L. inconspicuum* ($\chi^2 = 29.8$, d.f.=3, $p<0.001$); *L. inconspicuum* and *L. maccanni* ($\chi^2 = 20.2$, d.f.=3, $p<0.001$). *L. n. polychroma* was often associated with grasses (mainly tussocks), while the other two species were usually found in herbs and shrubs. Significantly, no *L. n. polychroma* or *L. inconspicuum* individuals were found in rock outcrops, although they were often found within a few metres of these features. Casual observation illustrated the strength of these habitat preferences. During this study I spent two summers in a hut on the banks of Burgan Stream. Among the many lizards I saw on the bank in front of the hut, I identified only *L. maccanni* and *L. n. polychroma*. On the comparatively level area of tussock grassland behind and to the sides of the hut I observed only *L. inconspicuum* and *L. n. polychroma*, whereas in the introduced grass around the base of the hut I observed only *L. n. polychroma*, on numerous occasions. There appeared to be a line of demarcation along the top of the stream bank, across which *L. inconspicuum* and *L. maccanni* seldom ventured.

Head sizes

The Mann-Whitney U test showed significant differences ($p<0.05$) in head size between most sex, age and species classes. Only three comparisons showed no significant differences in either head length or width: *L. n. polychroma* adult males vs *L. n. polychroma* adult females, *L. maccanni* adult males vs *L. maccanni* adult females, and *L. inconspicuum* subadults vs *L. maccanni* subadults.

Feeding ecology

The prey items eaten ranged in size from less than 0.1mm^3 to 1200mm^3 (this latter item was a cicada nymph). The K-S two-tailed tests showed no significant differences in prey size distributions between the areas in which *L. n. polychroma* was syntopic with either *L.*

Table 2 – Habitat utilization by the three skink species. Numbers of individuals (percentages in parentheses) of each species in four microhabitats.

Species	Microhabitat			
	Grasses	Herbs & shrubs	Rocks	Rock Outcrops
inconspicuum	2(7)	16(53)	12(40)	0(0)
maccanni	3(5)	33(52)	6(9)	22(34)
n.polychroma	34(70)	8(16)	7(14)	0(0)

inconspicuum or *L. maccanni*. In the only other type of area on which lizards were sampled for prey analysis, the three species were syntopic, and so all of the prey data were pooled in the K-S one-tailed test (Table 3). One female *L. inconspicuum* contained 41 out of the 134 prey items recorded from all adult females. This was most unusual, and the individual was removed from the analysis because its inclusion would have unduly biased the results. All three species utilized a large proportion of relatively small prey items (Fig. 2). The K-S tests show that most of the differences in prey size utilization were between subadults and adults (Table 3); subadults ate smaller prey than adults. There were relatively few differences between similar age classes of the three species.

The skinks ate a large range of invertebrates, including insects of most orders (Patterson, 1985). They also ate other skinks; *L. n. polychroma* remains were found in the stomachs of the other two species. However, this does not necessarily indicate interspecific predation. Only the tails of *L. n. polychroma* individuals were eaten, probably after becoming detached during aggressive encounters between the skinks. Although this behaviour was not observed directly, it has previously been noted in *L. zelandica* (=*L. n. maccanni*) by McCann (1955), and in *L. suteri* (Boulenger) by Towns (1975).

The relative population densities of most invertebrate orders, as indexed by the five invertebrate population estimates, did not vary greatly during the year, and so stomach content data from all skinks, with prey items classified to ordinal level or above were pooled (Fig. 3).

Spiders were the most important prey group, by number and volume, for *L. inconspicuum*; by number for *L. maccanni*, and by volume for *L. n. polychroma*. Berries were the second most important prey items by volume for *L. inconspicuum* and *L. maccanni* (Fig. 3). *L. n. polychroma* and *L. inconspicuum* ate greater volumes of spiders than of any other prey, whereas hemipterans were the most important prey by volume for *L. maccanni*. This high figure for hemipterans in *L. maccanni* is derived mainly from a few very large prey items, such as cicadas.

The results for the Mantel test showed that the frequencies of occurrence of prey taxa in the stomachs of *L. n. polychroma* and *L. maccanni* were different ($p<0.001$); the same applied to *L. inconspicuum* and *L. maccanni* ($p<0.05$). There was no significant difference in the pattern of prey taxa utilization between *L. n. polychroma* and *L. inconspicuum*.

The hours during which skinks were caught in pitfall traps are shown in Table 4. These activity records were standardized to "time since sunrise" (Pianka, 1973). The figures indicate that the three species were active at similar times of the day; but if there were any differences in their activity rhythms, not enough specimens were caught to detect them by this method. However, skinks observed in the greenhouse and in the study area displayed no discernible differences in these characteristics.

Table 3 – Statistical significance levels of prey size utilization for paired comparisons of skink age and sex classes (K-S one-tailed test). M = Adult males, F = Adult females, S = Subadults. n.p. = L. n. polychroma, inc = L. inconspicuum, mac = L. maccanni.

	n.p.(M)	n.p.(F)	n.p.(S)	inc(M)	inc(F)	inc(S)	mac(M)	mac(F)	mac(S)
n.p.(M):	–								
n.p.(F):	N.S.	–							
n.p.(S):	$p<0.001$	$p<0.01$	–						
inc(M):	N.S.	N.S.	$p>0.05$	–					
inc(F):	N.S.	N.S.	N.S.	N.S.	–				
inc(S):	N.S.	N.S.	N.S.	N.S.	N.S.	–			
mac(M):	N.S.	$p<0.01$	$p<0.05$	N.S.	N.S.	N.S.	–		
mac(F):	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	–	
mac(S):	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	$p<0.001$	–

Niche overlap

Because activity times differed relatively little among *L. n. polychroma*, *L. inconspicuum* and *L. maccanni*, the temporal niche dimension is not considered further. Accordingly, only two resources – microhabitat and prey size – are used in the present study to estimate total niche overlap (Table 5). Overlap was calculated for prey size by approximating prey size distributions using Weibull curves (Manly and Patterson, 1984). This technique avoids the pitfalls of subjectivity described by Schoener (1968). Values for the food niche overlap calculations are based on prey size data described earlier. Microhabitat overlap was calculated using Schoener's (1968) index. Since the two resources are probably independent (orthogonal), total niche overlap is likely to be the product of the separate unidimensional overlap measures (May, 1975). Using prey taxa in calculating total niche overlap for generalist opportunist predators leads to false results, since this dimension is related either to prey size or to microhabitat, and therefore is "included" in their overlap values (Krzysik, 1979). Accordingly, I did not calculate overlap values for prey taxa. However, an estimate of the relative degree of overlap by prey taxa between species pairs can be derived from the Mantel test. This shows a large overlap in prey taxa utilization between *L. n. polychroma* and *L. inconspicuum*, less overlap between *L. inconspicuum* and *L. maccanni*, and much less overlap between the remaining species pair (see under "Feeding Ecology" above).

As expected, the prey size overlap values paralleled those derived from the Kolmogorov-Smirnov one-tailed test. The only low overlap values found were for *L. maccanni* subadults compared with the other classes, and reflect the relatively

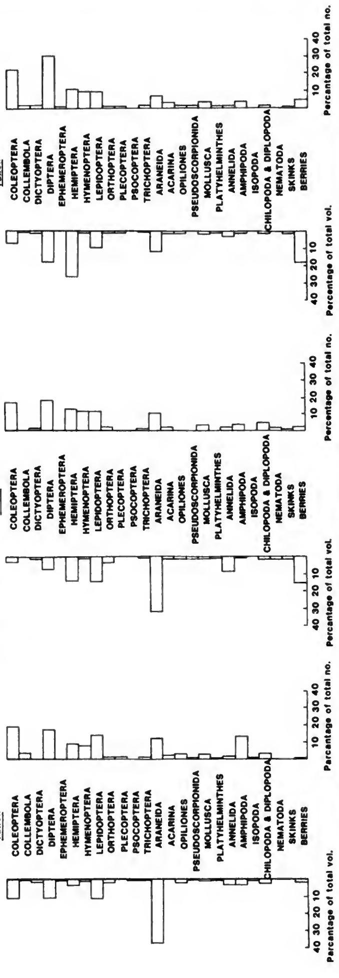
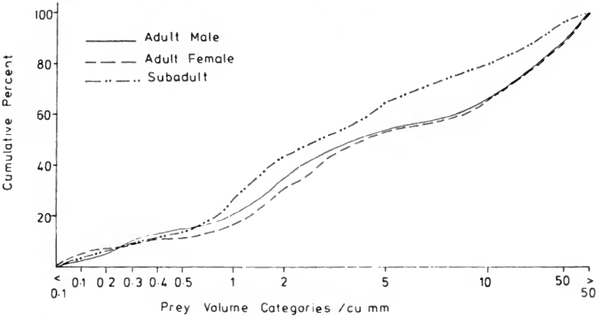
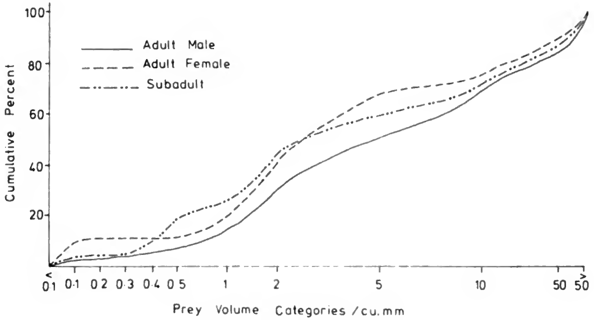


Fig. 2 – Percentage of prey taxa in stomachs of (left to right) *L. n. polychroma*, *L. inconspicuum*, *L. maccanni*, by volume and number.


Adult Male
Adult Female
Subadult
Cumulative Percent
100
80
60
40
20
< 0.1
0.1
0.2
0.3
0.4
0.5
1
2
5
10
50
> 50
Prey Volume Categories /cu mm


Adult Male
Adult Female
Subadult
Cumulative Percent
100
80
60
40
20
< 0.1
0.1
0.2
0.3
0.4
0.5
1
2
5
10
50
> 50
Prey Volume Categories /cu. mm

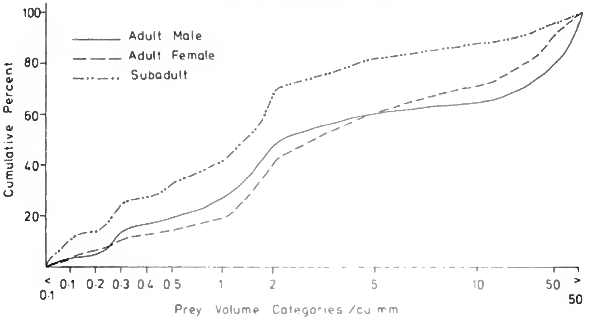

Adult Male
Adult Female
Subadult
Cumulative Percent
100
80
60
40
20
< 0.1
0.1
0.2
0.3
0.4
0.5
1
2
5
10
50
> 50
Prey Volume Categories /cu mm

Table 4 – Skink activity times

Time since sunrise	Number caught		
(hrs)	*maccanni*	*inconspicuum*	*n. polychroma*
0–1			
1–2			
2–3			
3–4			1
4–5			1
5–6	3	1	4
6–7		1	2
7–8			3
8–9	1	1	
9–10			2
10–11		1	1
11–12		2	1

Table 5 – Values of multiplicative total niche overlap and its components for the three skink species

Species pair	Microhabitat	Prey size	Total
n. polychroma – inconspicuum	0.373	0.970	0.362
n. polychroma – maccanni	0.304	0.855	0.260
inconspicuum – maccanni	0.656	0.845	0.554

large number of small prey items eaten by *L. maccanni* subadults.

The food and microhabitat overlap values for each species pair are given in Table 3, together with the multiplicative total niche overlap values. The greatest overall niche overlap is between *L. maccanni* and *L. inconspicuum*. However, the observed differences in microhabitat preference were large, and were the main reason for the low niche overlap value in all comparisons.

DISCUSSION

Aggressive behaviour

Although aggressive behaviour was recorded in these skinks, extensive overlapping of home ranges (Patterson, 1985) suggests that their aggression was not directed towards defending the entire home range, but rather towards defence of specific areas within the home range. Fighting has often been noted in other skinks, such as the Australian species *Sphenomorphus kosciuskoi* (Heatwole, 1976). Territorial exclusion among adults by aggressive behaviour has been previously observed in New Zealand skinks, including *Sphenomorphus pseudornatus* McCann (=*Cyclodina ornata* (Gray)) (Fawcett, 1964), *L. moco* (Dumeril and Bobron) (Whitaker, 1968) and *L. suteri* (Boulenger) (Towns, 1975). The interspecific differences in aggressive behaviour noted in the present study appeared to be related to different habitat preferences.

Separation of species by habitat

The distribution of species by habitat appeared to be primarily related to the physical

Fig. 3 – Prey size (volume of items in cubic millimetres) resource utilization spectra for *L. spp.* age and sex classes. Upper: *L. n. polychroma*; Middle: *L. inconspicuum*; Lower: *L. maccanni.*

structure of the environment, as noted in previous studies of habitat selection in lizards (*eg* Sexton *et al.*, 1964 and Heatwole, 1966).

I found that the three species in the study area could be identified by colour pattern. All three had stripes running the length of the body, but in *L. inconspicuum* and *L. maccanni* these were broken and often indistinct, whereas in *L. n. polychroma* they were always clearly defined (Patterson, 1985). In *L. n. polychroma*, a preference for tussocks associated with strong striping would be an adaptive combination, and is the same in specimens taken from tussock grassland in other parts of the range of the subspecies, but not in other habitats (Patterson and Daugherty, 1990).

The differences in prey taxa between *L. maccanni* and the other two species is also associated with different habitat preferences. For example, among the beetles eaten by all three species, a larger proportion eaten by *L. maccanni* were scirtids than in the other two species. Scirtids have aquatic larvae, and the adults are found near streams. Most *L. maccanni* specimens were obtained from gullies, which usually had streams at the bottom. Only a small proportion of individuals from the other two species was collected from these areas. Because more than 50% of *L. n. polychroma* specimens were obtained from areas where they were syntopic with *L. inconspicuum* alone, this could explain why *L. n. polychroma* displayed a significant difference in prey taxa utilization compared with *L. maccanni*. Allotopy could account for the similar difference between *L. inconspicuum* and *L. maccanni*. However, the difference between *L. n. polychroma* and *L. maccanni* is significant at $p < 0.001$, whereas the difference between *L. inconspicuum* and *L. maccanni* is significant at only $p < 0.05$. This indicates that the prey differences were not due solely to microgeographic factors. They may be caused by different foraging strategies, or competition (see below) for example.

Community structure and the avoidance of competition

Lizard species are usually separated by more than one niche dimension (Schoener, 1974). Niche separation between several other New Zealand skink species is based on food, microhabitat, and activity time (Whitaker, 1968; Gill, 1976). Other studies of lizard communities (summarized in Schoener, 1974) indicated that partitioning of microhabitat and food (size and/or taxa) was the most important factor minimizing competition in lizard communities, and thus contributing to stable coexistence.

In the present study, the differential utilization of habitats and food (size and taxa) also appears to be primarily responsible for reducing overlap among the species in the study area. *L. n. polychroma* and *L. inconspicuum* lived syntopically throughout a large section of the study area, despite extensive overlap in food utilization by taxa and size. Microhabitat was the only niche axis along which the two species differed significantly. This segregation of species by microhabitat appears to be caused partly or solely by interspecific aggression, which was noted in all three species in the wild. In the greenhouse experiment, *L. inconspicuum* and *L. maccanni* individuals chased *L. n. polychroma* individuals out of *Aciphylla* plants, whereas the reverse was not observed. *L. inconspicuum* and *L. maccanni* were more often found, in the field, in herbs and shrubs than was *L. n. polychroma*. Therefore, it is probable that *L. n. polychroma* was actively prevented from occupying microhabitats other than tussocks by the other two species (resource partitioning). This hypothesis is strengthened by the observation that *L. n. polychroma* lives in habitats other than tussock grassland in locations where the other species are not present, such as the North Island.

Specific site defence was also noted in disputes between *L. inconspicuum* and *L. maccanni*, but its effects are harder to determine than when confrontations involved *L. n. polychroma* and the other two species. *L. inconspicuum* and *L. maccanni* were generally allotopic, whereas the other two species pairs were generally syntopic. *L. maccanni* was usually found in gullies, whereas *L. inconspicuum* was generally in more open areas. At least one of the sites where *L. inconspicuum* and *L. maccanni* were syntopic appeared to be a boundary zone between the two populations. The data are consistent with competition theory: habitat separation may reflect ecological or evolutionary adjustments designed to reduce competition (Dueser and Shugart, 1979). Support for this hypothesis comes from the fact that the total overlap between *L. inconspicuum* and *L. maccanni* was greater than that between the other species pairs. This implies that competitive exclusion was most likely to occur between *L. inconspicuum* and *L. maccanni*. One of the aims of this study was to observe competition occurring in the wild. It proved almost impossible to observe interspecific interactions in the field, but I consider the greenhouse environment to be an accurate replica of the skinks' natural environment. The interspecific aggression I observed could be interpreted as interference competition. Therefore, although I did not achieve the original aim of studying behaviour in the field, I believe the experiment demonstrates a high probability of competition in the wild.

In a survey of community studies Toft (1985) found that competition was never the sole cause of resource partitioning in communities. It is, however, difficult to demonstrate that factors other than competition are also operating to produce resource partitioning in the lizard guild I studied. The species are so similar morphologically, physiologically and behaviourally that any differences that one might suggest as responsible for the observed niche differences are probably so minor as to be virtually undetectable by experimental means. The New Zealand lizard fauna contains many examples of species guilds, including several more diverse than the Rock and Pillar assemblage (Whitaker, 1968; Newman and Towns, 1985; Towns *et al.*, 1985). These are generally on northern offshore islands, but there is a guild of six congeneric skinks and one gecko species at Macraes Flat in the South Island (Towns *et al.*, 1985) that is in habitat very similar to the Rock and Pillar Range. Unfortunately, there has never been a detailed ecological study of this guild; but it looks as though there is little habitat overlap between species (Towns *et al.*, 1985). All synecological studies so far done on New Zealand skink guilds (Gill, 1976; Porter, 1987; Southey, 1985) have detected niche differences, mainly along the habitat axis. Although Southey saw no interspecific aggression, he noted superficial scars on his lizards, apparently caused by inter- or intraspecific fighting.

Character displacement

An observation supporting competitive exclusion is a pattern of community-wide character displacements – patterns of equal spacing in the size of some character, such as jaw length. These differences are frequently assumed to have resulted from coevolution (one species becoming larger, another smaller) to reduce interspecific competition by minimising the use of shared resources (Strong, 1983). Although evidence for character displacement has come from regular and/or large size differences in otherwise sympatric species (Schoener, 1982; Dayan *et al.*, 1989), the cause of these patterns is still uncertain (Pimm and Gittleman, 1990). The only traditional morphological indicators of coevolution measured in the present study, head width and length, differ between *L. n. polychroma* and the other two skink species by ratios of 1 : 1.1. Unfortunately, this size difference does not correspond with prey size distributions. There were few significant interspecific differences in prey size utilization between equivalent age classes, and those differences that existed were not always correlated with head size: *L. n. polychroma* adult females have smaller heads, but ate larger prey, than *L. maccanni* adult males. Also, *L. maccanni* subadults ate smaller prey than subadults of the other species, but have heads similarly sized to *L. inconspicuum* subadults, and larger heads than *L. n. polychroma* subadults.

Earlier studies have also shown that the relationship between skink head size and prey size is variable. Within *Anolis* species, for example, larger individuals ate larger food items than smaller individuals (Schoener, 1968). Pianka and Pianka (1976) showed that head length was correlated with prey size in Australian geckos. Larger species tended to eat larger prey than smaller species. However, Schoener and Gorman (1968) found that animals with identical head lengths from two *Anolis* species ate prey of different sizes. These observations illustrate the importance of finding out about the actual ecology of an animal before drawing conclusions based on only one set of ecological indicators, such as head sizes. Since I found no direct relationship between head size and prey size in the Otago skinks, I conclude that head size differences are unlikely to have arisen through coevolution within this skink community.

Many species of small vertebrates, including skinks, have become extinct in recent times due to predation by introduced mammals such as kiore (Worthy, 1991). These vanished species may have contributed to the lizard community structures observed today (Connell's (1980) "ghost of competition past"). However, there is little evidence that communities such as the ones I observed were more diverse in the past. On the contrary, the opening up of the tussock land by browsing and grazing herbivores has possibly allowed colonisation by new lizard species. I therefore propose an origin other than coevolution for the size distribution of the species I observed, which also explains how their habitat preferences arose.

A new hypothesis

Hardy (1977) suggested that New Zealand skink populations, geographically isolated during glaciations, subsequently became reproductively isolated. Then in post-glacial periods, the newly-formed species reinvaded the areas formerly occupied by the parent species. Current species distributions are consistent with this theory.

Although populations could have mixed along the coastline, it is interesting to note that *L. maccanni* and *L. inconspicuum* are very seldom found in this habitat today.

Glaciation is not the only factor that might have caused populations to become isolated. Towns *et al.* (1985) point out that species could have differentiated much earlier than Hardy proposed. Populations may have become isolated during mountain-building before the ice ages, or in tussock islands separated by forest before or during the ice ages. The skink species I studied have occasionally been found in forest, but only in small pockets of open bush with no undergrowth (Patterson, *pers. obs.*). Speciation could have occurred in a geologically brief time under these conditions.

Paterson (1978, 1980, 1981, 1982) proposed that members of a species share a common specific-mate recognition system (SMRS), which ensures mating within a population occupying its preferred habitat. The characters of the SMRS are adapted to function efficiently in this preferred habitat. A new species arises when all members of a small, isolated subpopulation of a parental species have acquired a new SMRS, which makes effective signalling impossible between members of the daughter and parental populations. Species-specific characters, such as head size and habitat preferences, develop in the isolated subpopulation during a relatively short period of adaptation to the prevailing conditions. Then the species spreads throughout its new habitat. Species descended from the same stock may often differ only in minor ways due to differences in the habitat in which speciation began. Behavioural characteristics might then become more pronounced when the species boundaries overlap, causing most, if not all, of the ecological differences in the Rock and Pillar community, for example.

Although Paterson's ideas are not widely accepted, and there is no evidence that an SMRS exists for the skinks in the present study, I think that it is unlikely that species such as *L. n. polychroma* and *L. inconspicuum* could live syntopically without possessing a means of avoiding interspecific mating. More research is needed on the ecology of New Zealand lizards to determine the validity of my hypothesis.

ACKNOWLEDGEMENTS

I am most grateful to my supervisors, Carolyn Burns and Donald McGregor, for their guidance during my research. Brian Niven and Bryan Manly helped greatly with the statistics, and David Towns, Michael Thompson and several anonymous reviewers provided useful comments on the manuscript. Ken Heckler of Gladbrook Station provided pleasant accommodation during fieldwork. Graeme Bremner directed me to the three-species site, and was a constant support throughout the study. The research was supported in part by the Miss E.L. Hellaby Indigenous Grasslands Research Trust.

REFERENCES

Andrews, R.M., 1971. *Food resource utilization in some tropical lizards.* Unpublished PhD thesis, University of Kansas, Kansas.

Barwick, R.E., 1959. The life history of the common New Zealand skink, *L. zelandica* (Gray, 1843). *Transactions of the Royal Society of N.Z.* 86: 331–380.

Braun-Blanquet, J., 1932. *Plant Sociology*. McGraw-Hill, New York.

British Ecological Society (1944). Symposium *The ecology of closely allied species*. Journal of Animal Ecology 13: 176–177.

Burt, W., 1943. Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* 24: 346–352.

Chesson, P., 1991. A need for niches? *Trends in Ecology and Evolution* 6(1): 26–28.

Connell, J.H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. *Oikos* 35:131–138.

Daugherty, C.H., Patterson, G.B., Thorn, C.J. and French, D.C., 1990. Differentiation of the members of the New Zealand *Leiolopisma nigriplantare* species complex (Lacertilia: Scincidae). *Herpetological Monographs* 4:61–76.

Dayan, T., Simberloff, D., Tchernov, E., and Yom-Tov, Y., 1989. Inter- and intraspecific character displacement in mustelids. *Ecology* 70(5): 1526–1539.

Dueser, R.D., and Shugart, H.H., Jr., 1979. Niche pattern in a forest-floor small mammal fauna. *Ecology* 60: 108–118.

Fawcett, J.D., 1964. *The life history and ecology of* Sphenomorphus pseudornatus. Unpublished MSc Thesis, University of Auckland, Auckland.

Fraser, D.F., 1976. Empirical evaluation of the hypothesis of food competition in salamanders of the genus *Plethodon*. *Ecology* 57: 459–471.

Gilbert, O., Reynoldson, T.B., and Hobart, J., 1952. Gause's hypothesis: an examination. *Journal of Animal Ecology* 21: 310–312.

Gill, B.J., 1976. Aspects of the ecology, morphology and taxonomy of two skinks (Reptilia: Lacertilia) in the coastal Manawatu, New Zealand. *N.Z. Journal of Zoology* 3: 147–157.

Hairston, N.G., 1989. Hard choices in ecological experimentation. *Herpetologica* 45: 119–122.

Hardy, G.S., 1977. The New Zealand Scincidae (Reptilia: Lacertilia); a taxonomic and zoogeographic study. *N.Z. Journal of Zoology* 4: 221–325.

Heatwole, H., 1966. Factors affecting orientation and habitat selection in some geckos. *Zeitschrift fur Tierpsychologie* 23: 303–314.

———— 1976. *Reptile Ecology*. University of Queensland Press, Queensland.

Holdsworth, D.K., 1981. *Yield and macronutrient content of water from the snow tussock grassland zone of eastern and Central Otago.* Unpublished PhD thesis, University of Otago, Dunedin.

Jaeger, R.G., and Walls, S.C., 1989. On salamander guilds and ecological methodology. *Herpetologica* 45: 111–119.

Krzysik, A.J., 1979. Resource allocation, coexistence and the niche structure of a streambank salamander community. *Ecological Monographs* 49: 173–194.

Manly, B.F.J., and Patterson, G.B., 1984. The use of Weibull curves to measure niche overlap. *N.Z. Journal of Zoology* 11: 337–342.

Mantel, N., 1967. The detection of disease clustering and a generalised regression approach. *Cancer Research* 27: 209–220.

Marcellini, D., and Mackey, J.P., 1970. Habitat preferences of the lizards, *Sceloporus occidentalis* and *Sceloporus graciosus* (Lacertilia: Iguanidae). *Herpetologica* 26: 51–56.

Mark, A.F., 1965. Vegetation and mountain climate. *In*: R.G. Lister and R.P. Hargreaves (Eds.): *Central Otago*, pp. 69–91. N.Z. Geographical Society, Caxton Press, Christchurch.

May, R. M., 1975. Some notes on estimating the competition matrix, α. *Ecology* 56: 737–741.

McCann, C., 1955. The lizards of New Zealand. Gekkonidae and Scincidae. *Dominion Museum Bulletin* 17: 1–127.

Miller, R.S., 1967. Pattern and process in competition. *Advances in Ecological Research* 4: 1–74.

Newman, D.G., and Towns, D.R., 1985. A survey of the herpetofauna of the northern and southern blocks, Great Barrier Island, New Zealand. *Journal of the Royal Society of N.Z.* 15: 279–287.

Nie, N.H., and Hull, C.H., 1981. *Statistical Package for the Social Sciences (SPSS): Update 7–9.* McGraw-Hill, New York.

Odum, E.P., and Kuenzler, E.J., 1955. Measurement of territory and home range size in birds. *Auk* 72: 128–137.

Paterson, H.E.H., 1978. More evidence against speciation by reinforcement. *South African Journal of Science* 74: 369–371.

———— 1980. A comment on "mate recognition systems". *Evolution* 34: 330–331.

———— 1981. The continuing search for the unknown and unknowable: a critique of contemporary ideas on speciation. *South African Journal of Science* 77: 113–119.

———— 1982. Perspective on speciation by reinforcement. *South African Journal of Science* 78: 53–57.

Patterson, G.B., 1985. *The ecology and taxonomy of the common skink* L. nigriplantare maccanni *in tussock grasslands in Otago.* Unpublished PhD Thesis, Otago University, Dunedin.

———— 1986. A statistical method of testing for dietary differences. *N.Z. Journal of Zoology* 13(1): 113–115.

Patterson, G.B., and Daugherty, C.H., 1990. Four new species and one new subspecies of skink, genus *Leiolopisma* (Reptilia: Lacertilia: Scincidae) from New Zealand. *Journal of the Royal Society of N.Z.* 20: 65–84.

Pianka, E.R., 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4: 53–74.

Pianka, E.R., and Pianka, H.D., 1976. Comparative ecology of twelve species of nocturnal lizards (Gekkonidae) in the Western Australian desert. *Copeia* 1976: 125–142.

Pimm, S.L., and Gittleman, J.L., 1990. Carnivores and ecologists on the road to Damascus. *Trends in Ecology and Evolution* 5(3): 70–73.

Porter, R., 1987. An ecological comparison of two *Cyclodina* skinks (Reptilia: Lacertilia) in Auckland, New Zealand. *N.Z. Journal of Zoology* 14: 493–507.

Root, R.B., 1967. The niche exploitation pattern of the blue-grey gnat-eater. *Ecological Monographs* 37: 317–350.

Schoener, T.W., 1968. The *Anolis* lizards of Bimini: resource partitioning in a complex fauna. *Ecology* 49(4): 704–726.

———— 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.

———— 1982. The controversy over interspecific competition. *The American Scientist* 70: 586–595.

Schoener, T.W., and Gorman, G.C., 1968. Some niche differences in three lesser Antillean lizards of the genus *Anolis*. *Ecology* 49: 819–830.

Sexton, O.J., Heatwole, H., Knight, D., 1964. Correlation of microdistribution of some Panamanian reptiles and amphibians with structural organization of the habitat. *Caribbean Journal of Science* 4(1): 261–295.

Silvertown, J., and Law, R., 1987. Do plants need niches? Some recent developments in plant community ecology. *Trends in Ecology and Evolution* 2(1): 24–26.

Southey, I.C., 1985. *The ecology of three rare skinks on Middle Island, Mercury Islands*. Unpublished MSc Thesis, Auckland University, Auckland.

Strong, D.R., 1983. Natural variability and the manifold mechanisms of ecological communities. *The American Naturalist* 122: 636–660.

Toft, C.A., 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985(1): 1–21.

Towns, D.R., 1975. Ecology of the black shore skink, *L. suteri* (Lacertilia: Scincidae) in boulder beach habitats. *N.Z. Journal of Zoology* 2: 389–407.

Towns, D.R., Daugherty, C.H., and Newman, D.G., 1985. An overview of the ecological biogeography of the New Zealand lizards (Gekkonidae, Scincidae). In: G. Griggs; B. Shine; H. Ehman (Eds.): *Biology of Australasian Frogs and Reptiles*, pp. 107–115. Surry Beatty, New South Wales.

Vadas, R.L., 1990. Competitive exclusion, character convergence, or optimal foraging: which should we expect? *Oikos* 58: 123–128.

Whitaker, A.H., 1968. The lizards of the Poor Knights Islands. *N.Z. Journal of Science* 11: 623–651.

Worthy, T.H., 1991. Fossil skink bones from Northland, New Zealand, and description of a new species of Cyclodina, Scincidae. *Journal of the Royal Society of N.Z.* 21:329–348.

Received 21 September 1990; accepted 17 December 1991

© Journal of the Royal Society of New Zealand, Volume 22, Number 2, June 1992, pp 107–122

New Zealand fur seals at the Antipodes Islands

Rowland H. Taylor*

The Antipodes Islands (49° 41′ S, 178° 47′ E) were discovered in 1800, and their once-abundant fur seals exterminated within 20 years. It was over 150 years before these animals were once more regularly found at the islands. Since the 1950s, New Zealand fur seals, *Arctocephalus forsteri*, have slowly increased in numbers, and now about 2000 (mostly yearlings and older juveniles) visit the islands each year in late-summer, although there are far fewer in winter. Very few breed at the Antipodes; seven pups found in 1985 were the first recorded there this century. The history of fur seals at Macquarie Island is very similar to that at Antipodes, but both contrast with the far more rapid recovery in numbers of fur seals elsewhere in the New Zealand region. It has been argued that the original fur seals of these two island groups may not have been *A. forsteri*, but a species more vulnerable to sealing, and this suggestion is re-examined and discussed. An alternative hypothesis is presented: that the two islands may never have supported large breeding populations of fur seals, of any species, but rather were traditional hauling grounds for many thousands of juvenile New Zealand fur seals.

Keywords: Arctocephalus forsteri, A. tropicalis, A. gazella, *exploitation, population recovery, population characteristics, breeding status, the Upland seal, Antipodes I., Macquarie I., Subantarctic*

INTRODUCTION

New Zealand fur seals (*Arctocephalus forsteri*) are now increasing around New Zealand's coast and southern outlying islands, following massive exploitation during the 19th century (Crawley, 1990). However, numbers at two traditional fur seal strongholds in the region, the Antipodes and Macquarie Islands, have been very slow to recover (Taylor, 1979; Shaughnessy and Fletcher, 1987), while those elsewhere, including the Bounty, Snares, and Open Bay islands, and many on the Stewart Island and Fiordland coasts, are growing fast (Wilson, 1974, 1981; Crawley and Wilson, 1976; Taylor, 1982, 1990; Crawley, 1990). The reasons behind these contrasts are open to speculation; so is the specific identity of the so-called "Upland" fur seal, recorded by early sealers from the Antipodes and Macquarie islands (Lesson, 1828). It has been suggested that the Upland seal was probably not *A. forsteri*, but either the subantarctic fur seal (*A. tropicalis*) or an undescribed and now-extinct species (Falla, 1948; Shaughnessy and Fletcher, 1987).

This paper summarises and discusses the discovery, exploitation, local extinction and recent recolonisation of fur seals at the Antipodes Islands (49° 41′ S, 178° 47′ E) based on historical information and field work carried out during seven expeditions to the islands between 1969 and 1990. Fur seal nomenclature follows Ridgway and Harrison (1981).

ANTIPODES ISLANDS

The Antipodes Islands are of volcanic origin, and lie about 740 km south-east of Dunedin and 220 km south of their nearest neighbours, the Bounty Islands (Fig. 1). They became part of New Zealand territory in 1870, were declared Flora and Fauna Reserves in 1961, and reclassified as Nature Reserves under the Reserves Act 1977.

---

* DSIR Land Resources, Department of Scientific and Industrial Research, Private Bag, Nelson, New Zealand

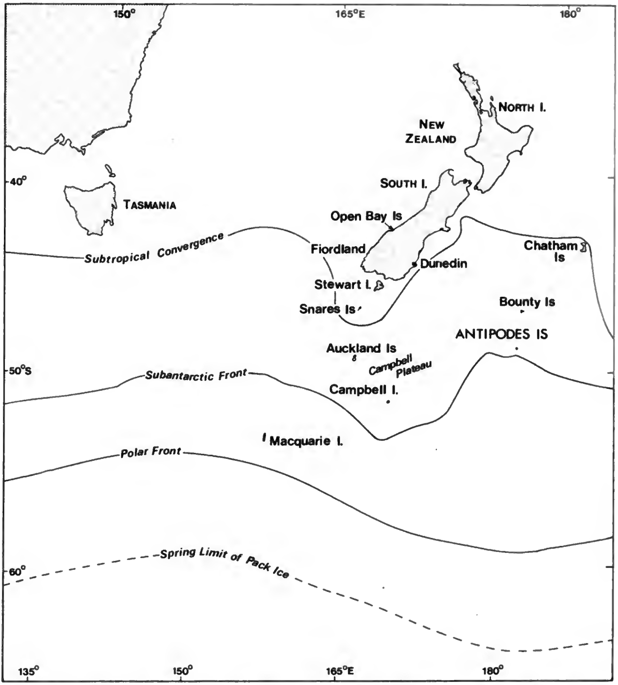


Fig. 1 – The position of the Antipodes and other southern islands, relative to the New Zealand mainland and oceanographic features.

The islands comprise one main island of about 2025 ha and six small islands and islets (Fig. 2). The main island is a broken, undulating plateau with hills rising to nearly 400 m. On both the slopes and the higher country the vegetation is mainly tussock interspersed with patches of sedges, ferns, herbaceous plants, and low shrubs. Only at Reef Point is there an area of gently sloping ground adjacent to the shore. Elsewhere, the coast is bounded by very steep slopes and cliffs from 20–150 m high. In places the cliffs are honeycombed with sea-caves of all sizes. Other conspicuous features of the shoreline are stacks and offshore rocks, deep narrow coves, smooth rock ledges, wave-cut platforms, steep tumbledown (talus) beaches, and a few short relatively sheltered beaches of small rounded boulders. The topography and vegetation of the islands are described by Warham and Johns (1975).

The Antipodes Islands are surrounded by waters colder than those about the other New Zealand islands. They lie close to the Subantarctic Front (Fig. 1) in a zone where surface water of relatively low temperature and salinity is driven northwards around the eastern side of the Campbell Plateau by the West Wind Drift (Heath, 1985).

PREVIOUS RECORDS OF SEALS AND SEALING AT THE ISLANDS

Discovery and exploitation

The Antipodes Islands and their then-teeming fur seal population were discovered in 1800 by Captain Waterhouse of HMS *Reliance*. Throughout the next quarter century, numerous sealers from Australia and North America called at the Antipodes, and well over one hundred thousand fur seals must have been taken. It is impossible to estimate the total kill with any accuracy. On many sealing voyages it was the practice to unload gangs on various southern islands as well as on the New Zealand mainland coast, and the tally of skins brought to Sydney at the end of each voyage often represented the yield from more than one locality. Also, deliberate misinformation on the source of seal skins was often spread to mislead competitors (McNab, 1907; Hall-Jones, 1945; Cumpston, 1968; Kerr, 1978). However, one sealing gang left at the Antipodes in 1804–05 took close on 60,000 skins, and there is ample documentation that these islands were among the richest fur sealing grounds in the southern hemisphere (Allen, 1899; McNab, 1907; Fanning, 1924).

Rapidly declining catches, and the discovery of the Auckland Islands in 1806 and Campbell and Macquarie Islands in 1810, appear to have soon drawn the focus of the sealing trade away from the Antipodes, and almost nothing was recorded of sealing voyages there after 1807. Judging from McNab's and Cumpston's well documented accounts, little credence can be given to the often quoted (*e.g.*, Sherrin, 1886; Allen, 1899; Thomson, 1927) report of an old Sydney sealer "that in two years (1814 and 1815) no less than 400,000 skins were obtained from Pennantipod, or Antipodes Islands alone"; for by then the fur seal populations of all the islands south of New Zealand were becoming depleted, and about 5000 skins in a voyage could be considered a good haul (McNab 1907; Cumpston 1968). In 1825, William Stewart visited the Antipodes Islands with the schooner *Prince of Denmark* during a 6 month search for a cargo in New Zealand waters. Notwithstanding Stewart's 20-year experience with New Zealand's southern islands and sealing, the voyage was a failure and he returned to Sydney with only 450 seal skins (McNab, 1907). Obviously, the southern fur seal trade was virtually finished.

Extinction

The Antipodes, along with other islands south of New Zealand, were visited by parties searching for ship-wrecked mariners in 1865 and 1868. Although published reports of these voyages (Norman and Musgrave, 1866; Armstrong, 1868) comment on the animal life, vegetation, and "necessaries of life" available for castaways at the various islands, they do not mention seals at Antipodes Islands. During August 1880 the *William and Jane* landed a sealing party at the Antipodes, which soon returned with the news that seals were not to be found. Later in the same year seven sealers from the schooner *Alert* were left ashore from 20 September to 7 November without finding "a sign of a seal upon the island" (Cumpston, 1955).

In 1886 a castaway depot was built on Antipodes Island and thereafter visited twice yearly by New Zealand Government vessels. No seals were reported seen at the islands by competent observers during any of these visits (*e.g.*, Fairchild, 1886; Reischek, 1888; Chapman, 1891; Carrick, 1892; Joyce, 1894; Lukins, 1896; Norman, 1918; Cockayne, 1904; Plunket, 1912; Waite, 1907; Archey, 1923; Oliver, 1927; Guthrie-Smith, 1936) until the service ceased in 1927 (Falla, 1950a). No seals were found by survivors of the wreck of the *Spirit of the Dawn*, who spent three months (4 September to 30 November) at Antipodes Island in 1893 (Anonymous, 1893), nor by the shipwrecked crew of the *Président Félix Fauré* who were there from 13 March to 12 May 1908 (Anonymous, 1908). It is thus adequately documented that within a few decades of the discovery of the Antipodes Islands, the once-abundant fur seal herds had been exploited to extinction.

In February and March 1926, the Antipodes Islands were visited by R. H. Beck and other members of the American Museum of Natural History's staff in the "Whitney South Seas Expedition" ship *France*. They reported, for the first time, a few elephant seals (*Mirounga leonina*), but no fur seals (Beck, 1928). The United States Coast Guard Icebreaker *Northwind* spent two days surveying the islands in early March 1947. Although parties were landed and helicopters flew over, no fur seals were seen (Rear Admiral C. W. Thomas, pers. comm., 1972).

Recolonisation

Fur seals may have visited the islands occasionally after 1890. In 1891, the Antipodes were visited by sealers during a two month (July and August) open season "with some result" (Chapman, 1893; Wilson, 1893). Captain Bollons (1927) summed up his experience of many years on Government Steamers visiting the island: "At the Antipodes seals are rarely seen. The indiscriminate killing in season and out of season in the early days of sealing had the inevitable result of annihilation of the species".

In 1950, a scientific expedition searching for fur seals remained at the islands from 4 – 10 November, and although the whole of the east coast was carefully searched and points on the west coast examined from the sea during a circumnavigation of the island, only one old male fur seal was found ashore in Ringdove Bay (Falla, 1950a, b, c).

In November 1962 and January 1965 staff of the New Zealand Oceanographic Institute made landings at Reef Point, where a few fur seals were sighted (E. W. Dawson and K. Lewis, pers. comm., 1972). When the Research Vessel *Eltanin* called at the Antipodes on 3 January 1967, fur seals were more numerous; P. Harper (pers. comm., 1972) observed a few hundred in the area of Reef Point and Stella Bay. My examination of photographs of fur seals taken during these visits shows the animals to be mostly yearlings and sub-adults.

OBSERVATIONS ON FUR SEALS IN 1969, 1978, 1983, 1985, 1989, AND 1990

Methods

I have studied fur seals at Antipodes Islands on each of five visits: 28 January to 10 March 1969; 9 November to 5 December 1978; 1 – 8 March 1985; 3 – 8 December 1989; and on 12 December 1990. In addition, fur seals were counted by members of the crew of HMNZS *Otago* in early April 1983, and by Carey (1990) during mid-October 1990.

I observed the diurnal rhythm of fur seals ashore at Reef Point and Stella Bay between 05.00 hours and 19.00 hours on 19 and 28 February 1969, to help interpret counts made at different times of day. Most of my other observations were made between 09.00 and 16.00 hours on days with good visibility. I divided the coastline into defined sectors (Fig. 2) and counted the seals in each. Whenever possible I classified fur seals as pups, yearlings, or others. Sometimes the "others" could be sub-categorised, but I did not attempt to identify the sexes, except the adult males.

I defined pups as young seals still in their dark natal coat, *i.e.*, less than 4 months old.

Since the yearling groups were such a conspicuous feature of the population in 1969, I made a special effort to identify this age class in subsequent years. The yearlings were distinguishable by their size (under one metre long), rounded heads, short pale coats, and habit of often associating together in compact groups both while ashore and in the water. True yearlings would have been about 14 months old during the 1969 and 1985 expeditions, and about 12 months old in 1978 and 1989. However, it is likely that sub-adults in their third year were sometimes placed in this category.

Searching procedures varied between the expeditions and were as follows:

1969: Between 28 January and 10 March, with help from Brian Bell, I searched the

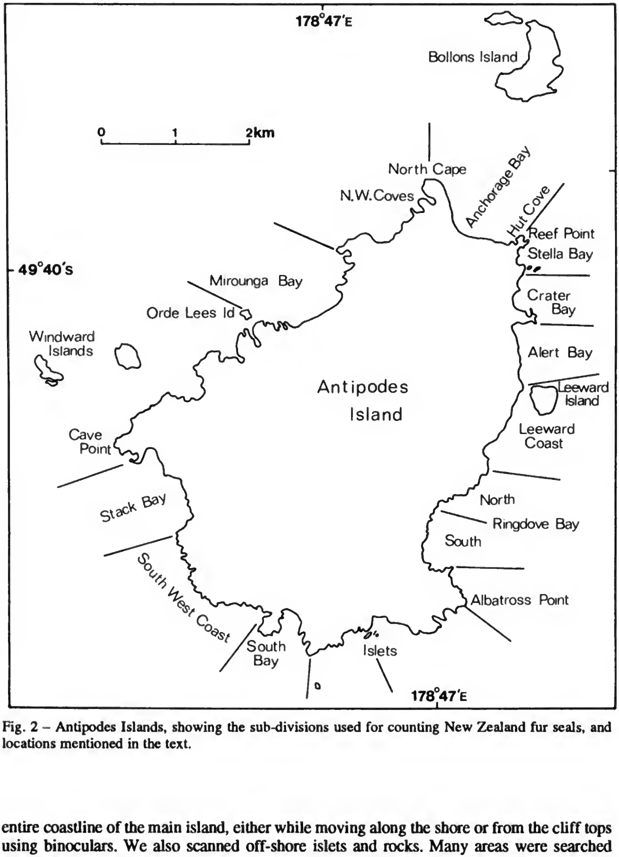


Fig. 2 – Antipodes Islands, showing the sub-divisions used for counting New Zealand fur seals, and locations mentioned in the text.

entire coastline of the main island, either while moving along the shore or from the cliff tops using binoculars. We also scanned off-shore islets and rocks. Many areas were searched twice during this period.

1978: I counted seals between 9 November and 5 December both from the sea, using small boats, and by landing. The survey included all outlying islets and stacks. On 20 November, I counted seals along the exposed coast from Albatross Point to the Windward Islands from a helicopter. All areas were searched at least twice during the expedition, firstly in the period from 9 to 20 November and again on 29 and 30 November.

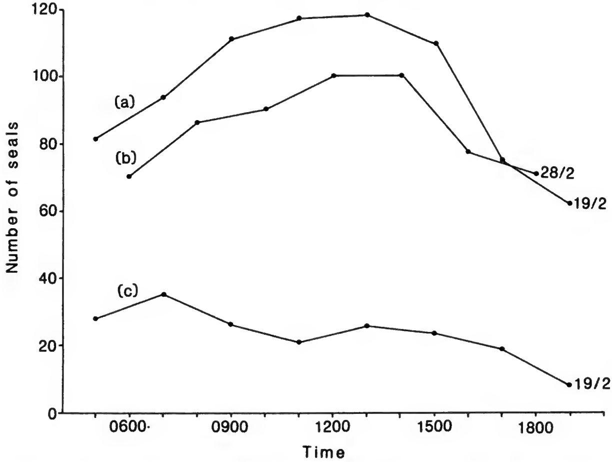


Fig. 3 – Diurnal variation in the total number of New Zealand fur seals (a and b) and yearlings (c) ashore near Reef Point, Antipodes Island, on 19 and 28 February 1969.

1983: 9 April. Fur seals were counted by RNZN personnel from rubber dinghies and from the land between Anchorage Bay and the southern end of Crater Bay.

1985: Helped by Richard Sadleir, I counted fur seals at Reef Point and in Stella Bay from the land several times between 1 and 4 March, and on the north and east coasts (from North Cape to Albatross Point) from a rubber dinghy on 3 March. I searched the remainder of the coastline, including all offshore islets and stacks, from a helicopter on 4 March.

1989: I counted fur seals at Reef Point and Stella Bay from the land several times between 3 and 8 December. I searched closely the rest of the east, north and west coasts and all islets, with numerous landings, from a rubber dinghy on 4 and 7 December. I checked (with less precision) the exposed south coast from the MS *Southern Cross* on 7 December.

1990: Carey (1990) counted fur seals between Anchorage and Crater Bays in the period 12 – 16 October. On 12 December I checked closely the south-east coast of the main island, from Leeward Island to South Bay, from a rubber dinghy for signs of breeding fur seals, but did not attempt to make a census.

Results

During February 1969, the highest numbers of fur seals were ashore in the early afternoon (Fig. 3), as is the case elsewhere among non-breeding seals on hauling-grounds (Stirling, 1968; Crawley, 1972), but the proportion of yearlings was highest at 07.00 hours. These observations confirmed the wisdom of confining census counts to between 09.00 and 16.00 hours.

Results of six censuses of fur seals at Antipodes Islands are summarised in Table 1.

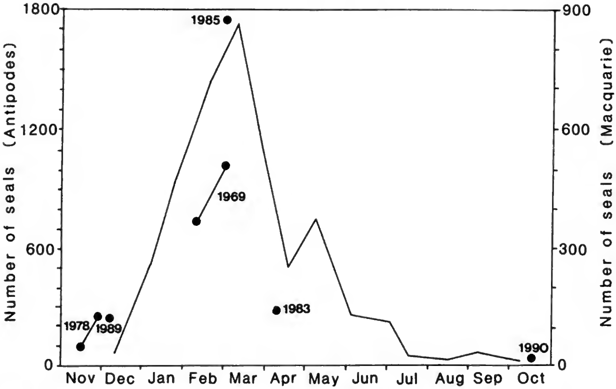


Fig. 4 – Seasonal variation in all censuses of New Zealand fur seals at Antipodes Islands from 1969 to 1990 (•) compared with the monthly variation in numbers of fur seals on North Head Peninsula, Macquarie Island, during 1981-82 (continuous line). Antipodes Island values for April and October were estimated from incomplete censuses in 1983 (see text) and 1990 (Carey, 1990). Macquarie Island data are from Shaughnessy and Fletcher (1987).

1969: In February/March about 1,100 New Zealand fur seals were present. About 46% were small yearlings, but there were no pups or other evidence of fur seals breeding locally (Taylor, 1969). The number of seals present increased by about 40% between early February and early March (Fig. 4). They were concentrated along the sheltered eastern shore between North Cape and Albatross Point, and only 47 were found on other parts of the coastline.

1978: The first counts, between 9 and 20 November, revealed 91 New Zealand fur seals, but by 29 November new animals boosted this number to 277 (Fig. 4), 54% of which were yearlings (Taylor, 1979). Numbers were still increasing in the vicinity of Reef Point until the expedition departed on 6 December. I saw no evidence of breeding and, although two or three mature bulls displayed territorial behaviour, only a few females were in the vicinity and there were no signs of harem formation. The yearlings were concentrated at Reef Point, the south end of Crater Bay, and to the north of Ringdove Bay (Fig. 5). At all of these sites there were flattish rocky shelves, easy access to higher ground, intertidal pools and sheltered water. One male *A. tropicalis* was ashore near Stella Bay (Taylor, 1990).

1983: On 9 April, 152 New Zealand fur seals were counted on the north-east coast between Anchorage Bay and the south end of Crater Bay. I have roughly estimated that about 270 (range 180 to 560) seals were then at the islands, based on the percentage of the total population found in this area during other censuses.

1985: I counted a total of 1,747 New Zealand fur seals on the entire coastline during the period 1 to 4 March, of which at least 60% were yearlings. On the west coast (Fig. 6) most were in tumbledown areas below the cliffs, whereas on the southern coast nearly all were on smooth rock ledges. The greatest numbers (1,400), including most of the young seals, were

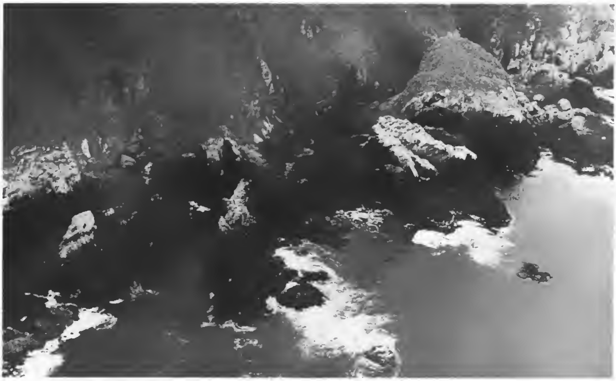


Fig. 5 – A typical haulout site of yearling and juvenile fur seals in North Ringdove Bay, Antipodes Island.

Fig. 6 – Mirounga Bay, on the west coast of Antipodes Island. Relatively few fur seals haul out on this coastline.

hauled out on the sheltered eastern side of the island. Fur seal pups were recorded for the first time; seven (all *A. forsteri*) were found at Reef Point. One of the smallest had a curvilinear length of 700 mm, indicating that it was about seven weeks old (Mattlin, 1981).

1989: I counted a total of 245 New Zealand fur seals between 3 – 7 December. Nearly all were on the eastern side of the island. None was seen along the south coast, but sea conditions did not allow a really close inspection there so it is possible that a few others may have been present. Yearlings made up over 60% of all seals seen. At Reef Point, four adult males were attempting to hold territories, but only one had a harem group of three females, and there were very few other adult females in the area. One male *A. tropicalis* was ashore at Reef Point (Taylor, 1990).

1990: Carey (1990) counted 14 New Zealand fur seals in the Anchorage Bay – Crater Bay sector during mid-October, which suggests that the total population was less than 50 at that time. Most of the fur seals I saw on 12 December were juveniles, and there was no sign of territory-holding bulls, harem groups, or young pups along the 7 km section of coast to the south and west of Leeward Island.

DISCUSSION

Recent recolonisation

Perhaps the most interesting feature of the fur seal population at the Antipodes Islands, when compared with all other populations in New Zealand territory, is its very slow recovery from past exploitation. For example, at the Bounty Islands, which are only 220 km to the north and where New Zealand fur seals were also exterminated during the sealing period, they have been breeding for at least 100 years and have steadily increased to over 20,000 (Taylor, 1982; and unpubl. data). By contrast, the vast majority of fur seals at the Antipodes are still non-breeding visitors. Most seals at the Antipodes Islands are yearlings and juveniles, which build up in numbers throughout the summer to a peak now reaching around 2,000 in March (Table 1). Breeding adults are still rare, and only a very few pups have been born at the Antipodes in recent years.

The situation at the Antipodes Islands is closely paralleled at Australia's Macquarie Island (Fig. 4), where New Zealand fur seals are present year-round, but do not breed. At Macquarie an influx of mainly young animals pushes fur seal numbers to a seasonal high between late-January and early-April (Gwynn, 1953; Johnstone, 1972; Shaughnessy and Fletcher, 1987). The fur seal population there has gradually increased from about 176 in 1950 to 1,222 in 1982 (6% per annum). When the index of abundance used at Macquarie Island (the maximum annual count of all animals between mid-February and early-April: Shaughnessy and Fletcher, 1987) is applied to the Antipodes Island counts (Table 1), it appears that the Antipodes population has increased at a slower rate of under 4% per year, from 1,020 in 1969 to 1,747 in 1985.

There could be many reasons why New Zealand fur seals are not breeding successfully at the Antipodes and Macquarie islands, but the most obvious relate to winter feeding conditions. If food is scarce around the islands in winter, then conditions may become marginal for the survival of nursing females and pups. Most *A. forsteri* pups are weaned by July or August (Crawley, 1990).

Around mainland New Zealand, *A. forsteri* feeds mainly on arrow squid (*Nototodarus sloanii*), octopus (*Octopus maorum*) and fish, although their diet varies seasonally (Street, 1964; Tate, 1981). It seems that very few squid are available to fur seals in southern New Zealand waters during winter (July to September), when commercial catches (weight caught and catch rate per trawl) decline by over 80% (Roberts, 1979). This winter period marks a change in habits of adult squid, when they spawn, possibly shift to deeper waters, and die at the end of their yearly life cycle. Also, it is the time when most squid in the next generation may be out of the seals' feeding range, or too small to be taken readily by seals (Tate, 1981). Near Dunedin, arrow squid was virtually the only cephalopod eaten by seals from February to May; in June, octopus became important, and rapidly replaced squid as the major cephalopod food (Tate, 1981). Octopus also live off the Bounty Islands, Snares Islands, and some other subantarctic islands, but have not been found in the colder waters of the Antipodes or Macquarie (D. Horning, pers. comm., 1978).

In the subantarctic, New Zealand fur seals also eat penguins (Bailey and Sorensen, 1962;

Table 1 – Total numbers of New Zealand fur seals and percentage of yearlings counted at the

	1969 (31 Jan-15 Feb)			1969 (22 Feb-10 Mar)		
	Total	Yearlings		Total	Yearlings	
Location	seals	n	%	seals	n	%
Bollons I	**0**	**0**	**0**	**6**	**0**	**0**
Anchorage Bay	**11**	**0**	**0**	**38**	**0**	**0**
Reef Pt / Stella Bay	**515**	**330**	**64**	**260**	**44**	**17**
Crater Bay	**101**	**5**	**5**	**230**	**many**	**–**
Alert Bay	**32**	**3**	**9**	**71**	**12**	**17**
Leeward Coast	**2**	**0**	**0**	**68**	**some**	**–**
North Ringdove Bay	**22**	**0**	**0**	**78**	**2**	**3**
South Ringdove Bay	**12**	**0**	**0**	**260**	**2**	**1**
Albatross Point	**0**	**0**	**0**	**–**	**–**	**–**
Albatross - Islets	**0**	**0**	**0**	**–**	**–**	**–**
Islets - South Bay	**0**	**0**	**0**	**–**	**–**	**–**
South Bay & Peninsula	**10**	**0**	**0**	**–**	**–**	**–**
Southwest Coast	**1**	**0**	**0**	**9**	**0**	**0**
Stack Bay	**0**	**0**	**0**	**0**	**0**	**0**
Cave Point - Orde Lees I.	**21**	**0**	**0**	**–**	**–**	**–**
Mirounga Bay	**7**	**0**	**0**	**–**	**–**	**–**
NW Coves	**0**	**0**	**0**	**–**	**–**	**–**
TOTALS	**734**	**338**		**1020+**		

Green *et al*., 1990). Both species of penguins at the Antipodes Islands, the erect-crested (*Eudyptes sclateri*) and rockhopper (*E. chrysocome*), leave the islands during the winter. Similarly at Macquarie, the departure of the fur seals in April and May coincides with the departure of the abundant smaller penguin species, the rockhoppers and royal penguins (*E. chrysolophus*). Of the two penguin species remaining at Macquarie island during the winter, the king (*Aptenodytes patagonica*) is too large to be likely prey for the fur seal, while the gentoo (*Pygoscelis papua*) lives there only in small numbers (Csordas and Ingham, 1965).

Fur seals are generally shallow divers. For six species the mean depth of dive has been measured at around 40 m, with maxima seldom exceeding 170 m (Gentry and Kooyman, 1986; Croxall *et al*., 1985). Physiological and behavioural evidence suggests that New Zealand fur seals also feed close to the surface, or on the bottom in relatively shallow water (Street, 1964; Wells, 1977). Compared with all other subantarctic islands to the south of New Zealand, both the Antipodes and Macquarie islands are surrounded by deep water close inshore. The smaller shelf area would suggest that benthic food may be less available. Such a conclusion is consistent with the findings that, during summer, New Zealand fur seals at Macquarie Island feed mainly on pelagic fish and penguins, and seldom on benthic fish (Green *et al*., 1990).

Very little has been recorded on the winter distribution of pelagic fish in the immediate vicinity of the Antipodes and Macquarie islands. However, it is perhaps significant that the Antipodes avifauna lacks the blue-eyed shag (*Leucocarbo* sp.), an inshore-fishing species resident on most other southern New Zealand continental shelf islands (Warham and Bell, 1979).

The Upland seal: a distinct species?

Falla (1948, 1962, 1965) found from contemporary accounts of early sealing activity that the Antipodes and Macquarie Islands "were traditionally the scene of the largest slaughter in the decade 1810 to 1820 and tradition further states that the seals of these two islands had a superior fur and were known as the 'Upland Seal'." He pointed out that despite the

Antipodes Islands (locations as shown in Fig. 2)

1978 (9-20 Nov)			1978 (29 Nov)			1985 (1-4 March)			1989 (3-7 Dec)		
Total	Yearlings		Total	Yearlings		Total	Yearlings		Total	Yearlings	
seals	n	%	seals	n	%	seals	n	%	seals	n	%
0	0	0	1	0	0	0	0	0	0	0	0
2	2	100	7	0	0	54	41	76	5	0	0
26	20	77	53	30	57	73	26	36	37	20	54
33	30	91	112	80	71	377	338	90	90	76	84
3	0	0	10	0	0	97	68	70	15	0	0
2	0	0	8	0	0	260	201	77	8	0	0
12	10	83	43	38	88	262	224	85	55	45	82
1	0	0	23	3	13	265	142	54	24	12	50
0	0	0	1	0	0	12	–	–	0	0	0
0	0	0	1	0	0	70	–	–	0	–	–
0	0	0	1	0	0	55	–	–	0	–	–
0	0	0	2	0	0	35	–	–	0	–	–
0	0	0	0	0	0	50	–	–	0	–	–
2	0	0	2	0	0	60	–	–	0	–	–
2	0	0	4	0	0	35	–	–	4	0	0
1	0	0	4	0	0	42	–	–	5	0	0
7	2	3	5	0	0	0	0	0	2	0	0
91	64		277	151		1747	1040+		245	153+	

indiscriminate exploitation of fur seals by the early sealers, these islands were the "only two localities in the region where stocks were completely wiped out". He concluded that the seal involved was possibly the Kerguelen fur seal (*A. gazella*) or the Amsterdam Island fur seal (*A. tropicalis*) and "not the New Zealand fur seal which occupied the rest of the [New Zealand] area and still survives in fair numbers".

When reporting the occurrence of a stray *A. tropicalis* at Macquarie Island in 1959, Csordas (1962) referred to Falla's findings and similarly suggested that the original stock on Macquarie and Antipodes Islands must have been relatively more vulnerable to sealing than were New Zealand fur seals, and may have belonged to the *tropicalis* group. Csordas stressed that "if the sealers being laymen and without taxonomic training, were able to distinguish two types of seals, then there must have been a notable difference between the two groups".

An early reference to the "Upland Seal" was published by Lesson (1828) and translated into English by Hamilton (1843) as follows: "the Americans regard many seals as fur-seals, which are unknown to naturalists, and are quite distinct. Thus, according to them, the fur-seal of Patagonia has a bump behind its head; that of California is of very large dimensions; the Upland Seal, or that which retreats far from shore, is small, and exclusively inhabits the Macquarie Islands and Pennantipodes; and finally, that of the south of New Zealand has other and distinct characters".

Shaughnessy and Fletcher (1987) have discussed the identity of the original seal of Macquarie Island. They concluded from the fact that some of the seal population was ashore during winter when Macquarie Island was first discovered, and from what is now known of *A. gazella*'s habits elsewhere, that the Upland seal was unlikely to have been that species.

Since Csordas's (1962) sighting of a male *A. tropicalis* at Macquarie Island in 1959, a small breeding population of that species has established there (Shaughnessy and Fletcher, 1987) and two stragglers have been found at the Antipodes, in 1978 and 1989 (Taylor, 1990). As suggested by Csordas (1962), these records could be interpreted as the Upland seal rediscovering its old haunts (Falla, 1965; Shaughnessy and Fletcher, 1987). However, as pointed out by Shaughnessy and Fletcher (1987), stragglers of *A. tropicalis* are not limited to

Macquarie and Antipodes Islands. Furthermore, I would argue that since *A. gazella* and *A. tropicalis* would have been well known to the Anglo-American sealers, from their voyages to the South Atlantic and Southern Indian Ocean islands, they would surely have recognised either species at Antipodes and Macquarie islands.

Shaughnessy and Fletcher (1987) considered that the Upland seal was not likely to be *A. forsteri* from Lesson's (1828) description of the seal as "small" and having distinct characters from the fur seal of southern New Zealand. They concluded that although "*A. tropicalis* is more likely to have been the Upland seal than *A. gazella* or *A. forsteri*, the possibility remains that it was another, extinct species of fur seal".

These hypotheses could be tested if subfossil remains of fur seals were found on the Antipodes or Macquarie Islands. Unfortunately, "a terrain of coastal rocks backed by peat beds ..... is a poor preservative" (Falla, 1965), and no useful bones have yet been discovered at either island (Falla, 1965; Shaughnessy and Fletcher, 1987; pers. obs.).

However, there is no strong evidence that the Upland seal was a distinct species, confined to the Antipodes and Macquarie Islands. If the seals on these two islands were so distinct in character from other southern fur seals, it is rather surprising that this was recorded only in Lesson's (1828) text, and not in the many contemporary sealing records reviewed by Cumpston (1968) and others. Although Macquarie Island reputedly "abounded with pups only" when it was discovered in winter 1810, their numbers may have been exaggerated, for as few as 827 appear to have been taken by eight men in the first 10 weeks of sealing on the island, from 18 July to 2 October (Cumpston, 1968). Furthermore, the reported presence of so-called "pups" is not proof that seals were breeding at the island, for these could have been yearlings born elsewhere.

The Upland seal: an alternative hypothesis

The alternative hypothesis presented here is that the Antipodes and Macquarie Islands may never have supported large breeding populations of fur seals of any species, but rather that they were hauling grounds for hundreds of thousands of juvenile New Zealand fur seals migrating each summer from breeding rookeries at the Bounty, Chatham, Auckland, and Campbell islands.

Reasons for this suggestion are:

(i) Such a summer migration of yearling and juvenile *A. forsteri* was recognised at Macquarie Island in 1950 (Gwynn, 1953), and apparently still continues there (Shaughnessy and Fletcher, 1987) and at the Antipodes Islands (present study).

(ii) Following the onslaught of sealing throughout the New Zealand region, Antipodes and Macquarie were the only islands from which fur seals disappeared completely and failed to return for many years. As breeding populations of New Zealand fur seals at the Chatham, Bounty, Campbell and Auckland Islands declined to low levels, there would be no pressures on non-breeding animals to migrate away from these rookeries during the summer. Fur seals took well over a century to re-populate the Antipodes and Macquarie islands, and this re-population corresponded with an exponential increase in numbers at many other breeding grounds (Crawley and Wilson, 1976; Taylor, 1982).

(iii) The "Upland seal" was said to retreat "far from shore". "Uplands" is a traditional North American sealers term for those areas which are inland from the breeding grounds of northern fur seals (*Callorhinus ursinus*), and where pups and juveniles congregate while the rookeries are occupied by breeding adults (Sherrin, 1886). For instance, Harvey (1889) wrote concerning the behaviour of the northern fur seal at the Pribilof Islands that "the younger males are prevented from landing [at the breeding rookeries] by the older, and are compelled either to stay in the water or to go to the uplands". It seems likely that the term "Upland seal" could simply have referred to an age class with distinctive habits (Fig. 7) rather than to a separate species. The yearlings and juveniles of most southern species similarly congregate away from the rookeries during the breeding season (Bonner, 1958, 1968; Crawley, 1972; Wilson, 1974; Condy, 1978; pers. obs.). For New Zealand fur seals, three types of colonies

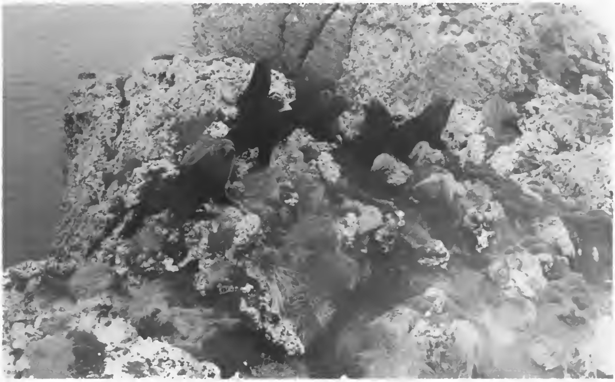


Fig. 7 – Upland seals? A group of juvenile New Zealand fur seals above Crater Bay, Antipodes Island, 9 November 1978.

have been defined: breeding rookeries, hauling grounds, and immature colonies (Wilson, 1974). To some extent, immature colonies are seasonal phenomena, although they always contain mainly young seals and very few adults during summer. The population composition at Antipodes and Macquarie Islands is similar to that described for immature colonies (Wilson, 1974).

(iv) The Upland seal was said to be smaller than the fur seal of the south of New Zealand. Adults of *A. gazella* or *A. tropicalis* are not noticeably smaller than adult *A. forsteri*, whereas a population of predominantly juvenile seals would obviously be so.

(v) It was claimed that the Upland seal had a "superior fur" (Falla, 1965). According to Backus (1889) the "best" fur seal pelts came from an age class known as "prime middling pups", with a length of about three feet. This is the size of New Zealand fur seals during their second year of life.

From my reasoning summarised above, I conclude that the Antipodes and Macquarie island fur seal populations were seen by early sealers as different from those of southern New Zealand simply because they were made up predominantly of yearling and immature seals – age groups which were known to them in the North Pacific as "Upland seals".

ACKNOWLEDGMENTS

I thank the Royal New Zealand Navy and the numerous expeditioners and colleagues who have helped with seal observations over many years, especially Brian Bell, Chris Robertson, Andy Cox, Richard Sadleir, Gerry Clark and Julian Matsen. The late Sir Robert Falla, Martin Cawthorn, Kerry-Jayne Wilson, Woody Horning and many others discussed ideas and provided unpublished information. Jocelyn Tilley drew the maps and graphs, and Martin Cawthorn, Malcolm Crawley, Kerry-Jayne Wilson and Peter Wilson commented on the manuscript.

REFERENCES

Allen, J. A., 1899. Fur-seal hunting in the southern hemisphere. *In* Jordan, D. S. (Ed): *The fur seals and fur-seal islands of the north Pacific Ocean*, part 3, pp. 307–319. Government Printing Office, Washington.

Anonymous, 1893. Rescue of castaways. Wreck of the Barque *Spirit of the Dawn. Otago Daily Times and Witness*, 5 December.

——— 1908. Wreck at the Antipodes. Twenty-two castaways. *Lyttelton Times*, 16 May: 9–10.

Archey, G., 1923. Notes on birds of the sub-antarctic islands of New Zealand. *Records of the Canterbury Museum* 2: 117–120.

Armstrong, H., 1868. Cruise of the brig *Amherst*. Official report. *N. Z. Government Gazette, Province of Southland* 6: 51–56.

Backus, M. M., 1889. Fur. *In*: *Encyclopaedia Britannica* (9th edition), vol. 9, pp. 836–839. Adam and Charles Black, Edinburgh.

Bailey, A. M., and Sorensen, J. H., 1962. Subantarctic Campbell Island. *Proceedings, Denver Museum of Natural History* 10.

Beck, R. H., 1928. *Beck's letters and journal, December 1923 – February 1928.* Unpublished volume in Ornithology Library, American Museum of Natural History, New York.

Bollons, I., 1927. Unpublished letter to the Secretary of Marine, 7 April 1927. New Zealand National Archives.

Bonner, W. N., 1958. Notes on the southern fur seal in South Georgia. *Proceedings of the Zoological Society of London* 130: 241–252.

——— 1968. The fur seal of South Georgia. *British Antarctic Survey Scientific Reports* 56.

Carey, P. W., 1990. Seals at the Antipodes Islands, October 1990. *In* Miskelly, C. M., Carey, P. W., and Pollard, S. D. (Eds): *Report, Antipodes Island Expedition 12–16 October 1990*, pp. 17–19. Department of Zoology, University of Canterbury, Christchurch.

Carrick, R., 1892. *New Zealand's lone lands, being brief notes of a visit to the outlying islands of the colony.* Government Printer, Wellington.

Chapman, F. R., 1891. The outlying islands south of New Zealand. *Transactions of the N. Z. Institute* 23: 491–522.

——— 1893. Notes on the depletion of the fur seal in the southern seas. *Canadian Record of Science*, October 1893: 446–459.

Cockayne, L., 1904. A botanical excursion during midwinter to the southern islands of New Zealand. *Transactions of the N. Z. Institute* 36: 225–333.

Condy, P. R., 1978. Distribution, abundance, and the annual cycle of fur seals (*Arctocephalus* spp.) on Prince Edward Islands. *South African Journal of Wildlife Research* 8: 159–168.

Crawley, M. C., 1972. Distribution and abundance of New Zealand fur seals on the Snares Islands, New Zealand. *N. Z. Journal of Marine and Freshwater Research* 6: 115–126.

——— 1990. Genus *Arctocephalus*. *In* King, C. M. (Ed): *The Handbook of New Zealand Mammals*, pp. 244–256. Oxford University Press, Auckland.

Crawley, M. C., and Wilson, G. J., 1976. The natural history and behaviour of the New Zealand fur seal (*Arctocephalus forsteri*). *Tuatara* 22: 1–29.

Croxall, J. P., Everson, I., Kooyman, G. L., Ricketts, C., and Davis, R. W., 1985. Fur seal diving behaviour in relation to vertical distribution of krill. *Journal of Animal Ecology* 54: 1–8.

Csordas, S. E., 1962. The Kerguelen fur seal on Macquarie Island. *The Victorian Naturalist* 79: 226–229.

Csordas, S. E., and Ingham, S. E., 1965. The New Zealand fur seal, *Arctocephalus forsteri* (Lesson), at Macquarie Island, 1949–64. *CSIRO Wildlife Research* 10: 83–99.

Cumpston, J. S., 1955. *Sub-antarctic by-ways. The history of Macquarie Island.* Unpublished manuscript in DSIR Land Resources Library, Nelson.

——— 1968. *Macquarie Island*. Australian National Antarctic Research Expedition scientific reports, series A (1) publication no. 93. Antarctic Division, Department of External Affairs, Melbourne.

Fairchild, J., 1886. Inspection of Antipodes and Bounty Islands and erection of castaway depot huts at both groups. *Appendix to the Journal of the House of Representatives* 1886. H24. p. 6.

Falla, R. A., 1948. The outlying islands of New Zealand. *N. Z. Geographer* 4: 127–154.

——— 1950a. Party completed detailed survey of outlying islands. *Evening Star, Dunedin*, 13 November 1950.

——— 1950b. Unpublished letter to the Secretary of Marine, 18 December 1950. N. Z. National Archives.

———— 1950c. Straight through from London. *N. Z. Listener*, 1 December 1950.

———— 1962. Exploitation of seals, whales and penguins in New Zealand. *Proceedings of the N. Z. Ecological Society* 9: 34–38.

———— 1965. Birds and mammals of the subantarctic islands. *Proceedings of the N. Z. Ecological Society* 12: 63–68.

Fanning, E., 1924. *Voyages and discoveries in the South Seas 1792–1832*. Marine Research Society, Salem, USA.

Gentry, R. L., and Kooyman, G. L., 1986. *Fur seals: Maternal strategies on land and at sea*. Princeton University Press.

Green, K., Williams, R., Handasyde, K. A., Burton, H. R., and Shaughnessy, P. D., 1990. Interspecific and intraspecific differences in the diets of fur seals, *Arctocephalus* species (Pinnipedia: Otariidae), at Macquarie Island. *Australian Mammalogy* 13: 193–200.

Guthrie-Smith, H., 1936. *Sorrows and joys of a New Zealand naturalist*. Reed, Dunedin.

Gwynn, A. M., 1953. Notes on the fur seal at Macquarie Island and Heard Island. *ANARE Interim Reports* 4. Antarctic Division, Department of External Affairs, Melbourne.

Hall-Jones, F. G., 1945. *Historical Southland*. H. & J. Smith, Invercargill.

Hamilton, R., 1843. Amphibious carnivora. *In* Jardine, W. (Ed): *The Naturalists Library*, vol. 8. Mammalia. Lizars, Edinburgh.

Harvey, M., 1889. Seal fisheries. *In*: *Encyclopaedia Britannica* (9th edition), vol. 21, pp. 581–583. Adam and Charles Black, Edinburgh.

Heath, R. A., 1985. A review of the physical oceanography of the seas around New Zealand – 1982. *N.Z. Journal of Marine and Freshwater Research* 19: 79–124.

Johnstone, G. W., 1972. A review of biological research by Australian National Antarctic Research Expeditions, 1947–71. *Polar Record* 16: 519–532.

Joyce, J. P., 1894. *Auckland, Campbell, and other islands (report on), and on their seals, and seal-rookeries*. Report to New Zealand Parliament. Government Printer, Wellington.

Kerr, I. S., 1978. Sealers in southern New Zealand. Unpublished. Manuscript papers 1685, Folder 2, in Alexander Turnbull Library, Wellington.

Lesson, R-P., 1828. Phoque. *In* Bory de Saint-Vincent, J. B. G. M. (Ed): *Dictionnaire Classique d'Histoire Naturelle*, vol. 13, pp. 400–426. Rey et Gravier, Paris.

Lukins, E., 1896. *Round Southern Isles*. Bond, Finney & Co, Nelson.

McNab, R., 1907. *Murihiku and the Southern Islands*. William Smith, Invercargill.

Mattlin, R. H., 1981. Pup growth of the New Zealand fur seal *Arctocephalus forsteri* on the Open Bay Islands, New Zealand. *Journal of Zoology, London*, 193: 305–314.

Norman, F. M. (*Ed*), 1918. *Memoirs of the life of the Right Hon. David, Seventh Earl of Glasgow, 1833–1915*. T. & A. Constable, Edinburgh.

Norman, W. H., and Musgrave, T., 1866. *Journals of the voyage and proceedings of H.M.C.S. Victoria in search of ship-wrecked people at the Auckland and other islands*. Government Printer, Melbourne.

Oliver, W. R. B., 1927. New Zealand's subantarctic isles. Unpublished. Dominion Museum, Wellington.

Plunket, Lord, 1912. The outlying islands of New Zealand. *United Empire, London*. January 1912: 18–28.

Reischek, A., 1888. Notes on the islands to the south of New Zealand. *Transactions of the N. Z. Institute* 21: 378–389.

Ridgway, S. H., and Harrison, R. J. (*Eds*), 1981. *Handbook of Marine Mammals*. Academic Press, London.

Roberts, P. E., 1979. Squid. *In* Elder, R. D., and Taylor, J. L. (Eds): Prospects and problems for New Zealand's demersal fisheries. *Fisheries Research Division Occasional Publication* 19: 35–41. N. Z. Ministry of Agriculture and Fisheries, Wellington.

Shaughnessy, P. D., and Fletcher, L., 1987. Fur seals, *Arctocephalus* spp., at Macquarie Island. *NOAA Technical Reports NMFS* 51: 177–188.

Sherrin, R. A. A., 1886. *Handbook of the fishes of New Zealand*, pp. 226–254. Wilson and Horton, Auckland.

Stirling, I., 1968. Diurnal movements of the New Zealand fur seal at Kaikoura. *N.Z. Journal of Marine and Freshwater Research* 2: 375–377.

Street, R. J., 1964. Feeding habits of the New Zealand fur seal. *N. Z. Marine Department Fisheries Technical Report* 9.

Tate, M. L., 1981. The autumn-winter diet of the New Zealand fur seal *Arctocephalus forsteri* (Lesson) with special reference to its cephalopod prey. Unpublished Diploma of Wildlife Management Thesis, University of Otago, Dunedin.

Taylor, R. H., 1969. Fur seals at Antipodes Islands 1969. *In* Sorensen, J. H. (Ed): New Zealand fur seals with special reference to the 1946 open season. *N. Z. Marine Department, Fisheries Technical Report* 42: 79–80.

——— 1979. Seals at the Bounty and Antipodes Islands. Unpublished DSIR Ecology Division File Report.

——— 1982. New Zealand fur seals at the Bounty Islands. *N. Z. Journal of Marine and Freshwater Research* 16: 1–9.

——— 1990. Records of subantarctic fur seals in New Zealand (Note). *N. Z. Journal of Marine and Freshwater Research* 24: 499–502.

Thomson, G. M., 1927. *Wildlife in New Zealand*, Part 1 – Mammalia. Government Printer, Wellington.

Waite, E. R., 1907. The southern islands – notes on the Governor's trip. *Weekly Press, Christchurch*, 27 February.

Warham, J., and Bell, B. D., 1979. The birds of Antipodes Island, New Zealand. *Notornis* 26: 121–169.

Warham, J., and Johns, P. M., 1975. The University of Canterbury Antipodes Island expedition 1969. *Journal of the Royal Society of N. Z.* 5: 103–131.

Wells, R. M. G., 1977. Observations on the haematology and oxygen transport of the New Zealand fur seal, *Arctocephalus forsteri*. *N. Z. Journal of Zoology* 5: 421–424.

Wilson, G. J., 1974. Distribution, abundance and population characteristics of the New Zealand fur seal (*Arctocephalus forsteri*). Unpublished MSc Thesis, University of Canterbury, Christchurch.

——— 1981. Distribution and abundance of the New Zealand fur seal, *Arctocephalus forsteri*. *Fisheries Research Division Occasional Publication* 20, N. Z. Ministry of Agriculture and Fisheries, Wellington.

Wilson, L. B., 1893. New Zealand seal-fisheries. *Appendix to the Journal of the House of Representatives New Zealand*. A1: 2–3.

Received 12 September 1991; accepted 3 December 1991

© Journal of the Royal Society of New Zealand,
Volume 22, Number 2, June 1992, pp 123–130

Status and longevity of the tuatara, *Sphenodon guntheri*, and Duvaucel's gecko, *Hoplodactylus duvaucelii*, on North Brother Island, New Zealand

Michael B. Thompson[1,4], Charles H. Daugherty[1], Alison Cree[1,5], Debbie C. French[1], James C. Gillingham[2] and Richard E. Barwick[3]

A herpetological survey in January 1988 of North Brother Island, Cook Strait, New Zealand, found populations of the tuatara (*Sphenodon guntheri*) and three species of lizards (*Hoplodactylus duvaucelii, Hoplodactylus maculatus*, and *Leiolopisma lineoocellatum*). Tuatara on North Brother I. are significantly smaller than *Sphenodon punctatus* on nearby Stephens Island, and the estimated density of 134/ha in good habitat is lower than reported on Stephens I. The total adult population size of tuatara is estimated at <300 adults. Two of the captured tuatara had been toe-clipped, one in 1957 and one in 1959. One *H. duvaucelii*, toe-clipped in 1958, had not grown in the 29 years since first capture; it was probably at least 36 years old. This may represent the longest documented survivorship of a lizard in nature.

Key words: tuatara, Sphenodon guntheri, Sphenodon punctatus, *Duvaucel's gecko,* Hoplodactylus duvaucelii, *density, New Zealand, North Brother I.*

INTRODUCTION

The Brothers are a group of small islands in Cook Strait, New Zealand. They are steep, windswept and support little vegetation apart from low shrubs on a few sheltered faces, and herbs and grasses elsewhere. North Brother I. (41° 07'S; 174° 27'E) has an area of about 4 ha (Newman, 1982), and a lighthouse. It also has populations of tuatara, *Sphenodon guntheri*, and of three species of lizards, the geckos *Hoplodactylus duvaucelii* and *H. maculatus*, and the skink *Leiolopisma lineoocellatum* (Barwick, 1982; Newman, 1982). All these reptiles are endemic to New Zealand.

H. duvaucelii was the subject of an intensive population study from 1957–59, when 301 individuals were uniquely marked by toe-clipping (Barwick, 1982). At the same time, 21 tuatara and some *H. maculatus* were also marked. A subsequent visit in 1968 permitted recovery of two previously marked *H. duvaucelii*, resulting in a minimum age estimate for one of 19 years (Barwick, 1982).

North Brother I. supports the only known population of *S. guntheri*, and is an important refuge for *H. duvaucelii*, which, since its extinction on the mainland, is now restricted to islands, most of which are off the north coast of the North I. In Cook Strait, *H. duvaucelii* survive on only seven islands, and the other species of tuatara, *S. punctatus*, on only four. The status of populations of *H. duvaucelii* in the Cook Strait region has not been investigated

---

[1] School of Biological Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand

[2] Department of Biology, Central Michigan University, Mt Pleasant, Michigan 48859, U.S.A

[3] Department of Zoology, Australian National University, P.O. Box 4, Canberra, A.C.T. 2600, Australia

[4] Present address: Zoology (A08), School of Biological Sciences, University of Sydney, N.S.W. 2006, Australia

[5] Present address: Department of Zoology, Otago University, Dunedin, New Zealand

since the work of Barwick. Accordingly, we conducted a herpetological survey of North Brother I. to: (a) confirm the continued presence of tuatara and lizards on the island; (b) assess the size (correlated with age: Dawbin, 1982a) structure of the tuatara population; (c) look for evidence of continued successful breeding of tuatara; and (d) try to locate any tuatara or geckos marked in the 1950's to obtain further information on the longevity of these species.

MATERIALS AND METHODS

The survey was conducted from 21 to 24 January, 1988. On arrival, we made a daylight reconnaissance of the whole island to establish likely search areas and to locate sites where reptiles had been caught in previous surveys by Barwick. During our three nights on the island, we captured by hand all tuatara and large *H. duvaucelii* observed. We focused on large rather than small *H. duvaucelii* because of our interest in recapturing animals marked 30 years ago. When time permitted, some large *H. maculatus* were also examined for previous marks. Our capture efforts were concentrated primarily on the area studied in detail by Barwick (1982), but the entire island was surveyed at least once at night during the visit. During the day we noted the presence and approximate abundance of *L. lineoocellatum*, but conducted no other studies on this species.

We recorded the cloacal temperature of each individual *S. guntheri* and *H. duvaucelii* caught, and the air temperature approximately 5 cm above the site of capture with a cloacal thermometer (made by Miller & Webber Inc, NY, USA). An identifying number was written on the flanks of each individual with a felt-tipped pen; the capture point was marked; and the animal was taken to the field laboratory. There, each was measured to the nearest 1 mm with a ruler [snout-vent length (SVL), vent-tail length (VT), and length of regenerating portion of tail, if any (R)], weighed to the nearest gram with a spring balance, and examined for toe-clips. Unmarked animals were uniquely marked by toe-clipping. Blood samples for genetic analysis were taken from the caudal artery or vein of both tuatara (Daugherty *et al*., 1990) and geckos (Hitchmough, unpubl. data) using a syringe and needle. All individuals were returned to their point of capture as soon as possible after processing (<3h), except for two *H. duvaucelii* taken to be deposited as voucher specimens for the National Museum of New Zealand, after study in the School of Biological Sciences, Victoria University of Wellington.

On the second and third nights, any tuatara marked previously by us were noted so that a population estimate could be calculated using a modified (weighted mean) Petersen method (Begon, 1979). All tuatara seen in the main search area were caught and processed, except for three that escaped down burrows; that is, there was no deliberate selective capture. Juveniles were seen and captured infrequently, and our estimates of density exclude the few juveniles we encountered. Only tuatara caught in the main search area at the top of the island (about 1.7 ha) were included in the analysis of density. Equal catchability of individuals in the population was tested by comparison of our captures with a truncated Poisson distribution using χ^2 (Caughley, 1977).

Data on size distribution of tuatara were compared with data collected on *S. punctatus* on Stephens I. (by M.B.T.) in October 1985 using a G-test (Sokal and Rohlf, 1981). In the Stephens I. sample, all adult females encountered (n = 239) were included, but large males (n = 70) were preferentially collected over small males. All were measured in the same way as those caught on North Brother I.

RESULTS

Tuatara

Data were recorded on 112 *S. guntheri* (70 males, 35 females, 6 juveniles, and 1 hatchling). Animals were considered juvenile when the secondary sexual characteristics (*i.e.*, relatively large head and well developed crest with fleshy base in males; small head and small crest in females: Dawbin, 1982a) were not sufficiently developed to allow sex to be determined.

Table 1. Measurements of size of two tuatara and one gecko marked in the 1950s and recaptured in 1988 on North Brother I. SVL = snout-vent length; VT = vent-tail length; R = length of tail regeneration.

Species/ sex	Date	SVL (mm)	VT (mm)	R (mm)	Mass (g)
S. guntheri	22–8–57	197	154	68	283
female	21–1–88	197	158	69	240
S. guntheri	25–8–59	102	108	0	42
male	21–1–88	174	191	0	225
H. duvaucelii	18–5–58	111	111	0	40
female	23–1–88	109	100	43	42

One female tuatara marked in 1957 was recaptured (Table 1). Our measurement of SVL gave an identical figure (197 mm) to the measurement taken 30 years previously. We assume she had reached full size when first captured. A male tuatara marked in 1959 was also recaptured (Table 1). He had grown 72 mm in SVL in 28.5 years, an average rate of 2.5 mm/yr.

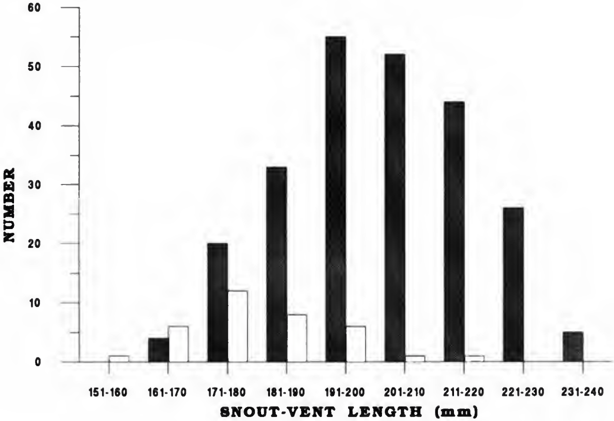
The modal size class (SVL) of adult female tuatara on North Brother I. is 20 mm smaller than that of tuatara on Stephens I. (Fig. 1), and the population size structures of the females on the two islands are significantly different ($G_{[7]} = 60.48$, $p < 0.001$; Sokal and Rohlf, 1981; comparison based on eight 10 mm size classes from 160 mm upward, n = 34). Although no similar assessment can be made for males, because of the selective sampling on Stephens I., the maximum SVL for both sexes on North Brother I. is at least 20 mm smaller than on Stephens I. (Fig. 1). The largest male collected on North Brother I. had a SVL of 246 mm, and the heaviest weighed 655 g; the largest female was 213 mm and 323 g.

Tuatara in the population were equally catchable ($\chi^2 = 2.912$, d.f. = 2, $p > 0.10$). The weighted mean Petersen estimate of population density was 227 individuals (s.d. = 59) for our 1.7 ha study area, or about 134 tuatara per ha. To estimate the total adult population size for the entire island, we assumed that (a) the total area of high quality habitat (*c.* 2.2 ha) had the same density of tuatara as the study site; and (b) the density of tuatara on the remainder of the island (*c.* 1.8 ha) was extremely low (we saw only one in this area). Our calculations exclude the one hatchling we found, as is done commonly in other estimates for tuatara, because it is usually impossible to avoid inadequate sampling of young animals (Newman, 1986). Our search area contained most of the prime habitat on North Brother I., *i.e.* it included the area covered by low growths of *Coprosma repens* and *Hebe* sp. Thus, the density of adult tuatara we estimate to live on our study site cannot be extrapolated to the entire area of the island (*i.e.* 4 ha × 134 tuatara/ha). Rather, we consider that there are probably fewer than 300 adult tuatara on North Brother I.

In November-December 1987, a resident lighthouse keeper recorded nesting activity of tuatara on North Brother I. in open areas adjacent to buildings and on tracks that are within the area vegetated by low shrubs. We examined these sites in January 1988, and found one nest containing live eggs, and two shells full of material assumed to be faeces of an invertebrate predator or scavenger.

H. duvaucelii

The 22 *H. duvaucelii* (10 males, 11 females, 1 juvenile) that we measured are not a random sample, because we concentrated on collecting large animals which may have been marked in the 1950s. Many other specimens were examined for toe-clips and released immediately. We found one female that had been toe-clipped as an adult in 1958 (Table 1). Our interpretation of the field notes of R.E. Barwick from 1958 indicates that we located this specimen within



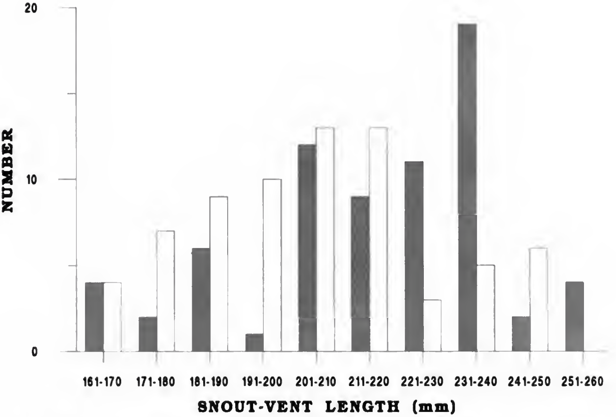


Fig. 1 – Above: Size distribution of female tuatara from Stephens I. (n=239) and North Brother I. (n=35). Below: Size distribution of male tuatara from Stephens I. (n=70) and North Brother I. (n=70). Shaded bars, Stephens I.; open bars, North Brother I.

5 m of the site where it was originally captured, possibly on the same rock. It had lost and regrown its tail, but had not increased in SVL. We recorded a 2 mm reduction in SVL (Table 1), but such a small deviation from the original measurement is within the limits of measuring accuracy for this species (Barwick, 1982).

Other lizards

H. maculatus was observed frequently in the study area at night. Many *L. lineoocellatum* were observed basking on paths, walkways, and exposed rocks during the day. However, no attempt was made to estimate numbers of these species.

Body temperatures

Body temperatures of tuatara and geckos captured between 2140 – 0325 hrs New Zealand Daylight Saving Time were usually within 1° C of ambient air temperature. The range of body temperatures was 9.5 – 18.2° C.

DISCUSSION

Status of populations

Results of our survey indicate that North Brother I. continues to support apparently healthy populations of three species of lizards, *L. lineoocellatum, H. maculatus* and *H. duvaucelii*. The high total numbers (probably several hundred), and apparent extreme longevity of *H. duvaucelii*, confirm that North Brother I. must continue to be considered a refuge of conservation importance for this species.

The density of tuatara in our study site is low (227 individuals/1.7 ha) compared with estimates for *S. punctatus* of 415/ha (Carmichael *et al*., 1989) and 480/ha (Crook, 1975) in sheep pasture on Stephens I., and 1,618/ha (Newman, 1982, 1987) and 2,015/ha (Carmichael *et al*., 1989) in forest on Stephens I. The average density over the whole of North Brother I. is likely to be even lower, as much of the remaining area is bare rock.

Although only 7 hatchling or juvenile tuatara were caught, their presence confirms that tuatara are reproducing successfully on North Brother I., and that the level of recruitment may be relatively high. Hatchling and juvenile tuatara are captured relatively infrequently, even on islands where recruitment is well documented (Newman, 1986). On some islands recruitment may be suppressed entirely by Polynesian rats, *Rattus exulans* (Cree and Daugherty, 1990).

The densities of tuatara are not only lower on North Brother I. than on Stephens I.; there are also notable differences between individuals on the two islands. Most tuatara on North Brother I. exhibit the very vivid white or light green spots on a greenish background to which the specific name "*punctatus*" refers. This colour pattern is relatively infrequent on Stephens I., where a great range of background coloration (*e.g*., green, brown, black, pink, rust) and pattern is found. Tuatara on North Brother I. are also generally smaller than on Stephens I. On Stephens I., *S. punctatus* attain maximum size in 25–35 years (Castanet *et al*., 1988), or possibly twice that (Dawbin, 1982a). By these criteria the female *S. guntheri* that we recaptured on North Brother I. that had been marked in 1957 was at least 60 years old, although it had a SVL 17 mm smaller than the mean size of the smallest mature *S. punctatus* from Stephens I. Using the growth rate estimated by Dawbin (1982a) for *S. punctatus* from Stephens I., the recaptured male *S. guntheri* would have been at least four years old when marked in 1959. Hence, at a minimum age of 33 years, it was probably still growing, as it was the seventh smallest male in our sample of 70. Thus, tuatara on North Brother I. may grow for a longer period than found by Castanet *et al*. (1988) for Stephens I., who therefore disputed Dawbin's (1982a) longer estimate of the growth period. The alternative explanation, that there is a great range of sizes at sexual maturity, we consider unlikely; *S. punctatus* on Stephens I. shows no such ranges of sizes (Dawbin, 1982a).

The reason for the observed difference in size and the possible difference in growth rate, between *S. guntheri* on North Brother I. and *S. punctatus* from Stephens I. are not clear. The differences could be species-specific, but this is not likely. *H. duvaucelii* is not found on Stephens I., but individuals of this species on North Brother I. are substantially smaller than on northern islands. This was attributed by Barwick (1982) to a possible latitudinal effect of temperature. However, the differences in the size of tuatara of North Brother I. and of Stephens I. are unlikely to result from temperature differences, because the islands are at approximately the same latitude and within sight of one another.

However, there are important differences between the two islands. For example, canopied forest is present only on Stephens I. This difference in habitat may affect the composition and abundance of prey for tuatara. The important dietary items of tuatara on Stephens I. (Walls, 1978, 1981) are beetles, some other invertebrates, lizards, and fairy prions, which are also abundant on North Brother I. However, tree weta (*Hemideina crassicruris*), a large orthopteran and a preferred food item for tuatara (Walls, 1981), are much scarcer on North Brother I. than on Stephens I. (Moller, 1985). We saw no tree weta on North Brother I. Therefore, differences in size and growth rate of tuatara on Stephens I. and North Brother I. cannot be attributed to species identity before the influence of food abundance and/or quality is investigated.

Longevity

Our most important result is the recapture of one *H. duvaucelii* 29 years and 8 months after first capture. Age to sexual maturity for the species on North Brother I. is seven years (Barwick, 1982). Therefore, this individual must have been at least 36 years old when recaptured. The previous estimate of maximum longevity for *H. duvaucelii* in nature was a full-grown female first marked in 1956 and recaptured in 1968, when it must have been at least 19 years old (Barwick, 1982). Our minimum age estimate extends this record by 17 years. A lengthy lifespan may be generally characteristic of the genus *Hoplodactylus* in New Zealand; a minimum estimate of longevity in wild *H. maculatus* on mainland New Zealand is 17 years (Anastasiadis and Whitaker, 1987), and up to 33 years in captivity (Meads, 1982).

Apart from the data on *H. maculatus* (Meads, 1982), the 36 year lifespan for *H. duvaucelii* is more than 20 years longer than any longevity records reported for lizards in the more benign conditions of captivity (Bowler, 1977). The only longer lifespan known to us for a lizard is for a slow worm, *Anguis fragilis*, that achieved an age of 54 years in captivity (Schmidt and Inger, 1957). Longevity in nature is difficult to assess, because field studies seldom follow marked individual lizards for decades. Equally remarkable is the recapture of the *H. duvaucelii* at virtually the same location at which it was first marked, indicating a tenacious site fidelity.

The long lifespan of tuatara has been well documented (Dawbin, 1982a), as have its other unusual attributes (Dawbin, 1982b). The discovery of very long life expectancy in *H. duvaucelii*, which has a geographic distribution similar to that of tuatara (Pickard and Towns, 1988), reinforces the suggestion that further studies of lizards should be implemented for comparison with tuatara living in the same habitat (Saint Girons, 1980; Gans, 1983).

Long lifespan in a protected species also has consequences for conservation policy. As in many other long-lived animals, tuatara reproduce relatively infrequently (Cree and Daugherty, 1990) and so may require extremely long periods to recover from reductions in numbers resulting from a disturbance (*e.g.* an invasion of rats onto North Brother I.). As an island reserve of high importance to several taxa of endemic New Zealand reptiles, and containing the only known population of *S. guntheri*, North Brother I. will require the highest level of conservation protection in the future.

ACKNOWLEDGMENTS

We are grateful for financial support provided by the Zoology Department, the Vice-Chancellor's office, and the Internal Research Committee, Victoria University of Wellington; the New Zealand University Grants Committee; World Wide Fund for Nature-New Zealand; the New Zealand Department of Conservation; and the New

Zealand Lottery Board. Ian Hargraves, Lighthouse Keeper, made observations on nesting and encouraged us to visit the Brothers. The lighthouse keepers on the Brothers during our trip, Bill Meginnis and Tim Watson, extended many courtesies and warm hospitality. The Marine Division, Ministry of Transport, arranged transport to the island. Collection of field data from Stephens I. was assisted by B. Blanchard, D. Brown, P. Carey, R. Delaney, M. Hurst, and D. Stotter. We thank A.H. Whitaker for useful discussion, and for the reference to longevity in *Anguis fragilis*, and D.G. Newman and D.T. Towns for critical review of the manuscript. Studies were conducted under permit from the New Zealand Wildlife Service (Department of Internal Affairs) and its successor, the Department of Conservation.

REFERENCES

Anastasiadis, J.M., and Whitaker, A.H., 1987. Longevity of free-ranging *Hoplodactylus maculatus* (Reptilia:Gekkonidae). *N.Z. Journal of Ecology* 10: 141–142.

Barwick, R.E., 1982. The growth and ecology of the gecko *Hoplodactylus duvauceli* at The Brothers Islands. *In* D.G. Newman (Ed): *New Zealand Herpetology*, pp. 377–391. New Zealand Wildlife Service Occasional Publication Number 2.

Begon, M., 1979. *Investigating Animal Abundance*. Arnold, London.

Bowler, J.K., 1977. *Longevity of Reptiles and Amphibians in North American Collections*. Society for the Study of Amphibians and Reptiles, Lawrence, Kansas.

Carmichael, C.K., Gillingham, J.C., and Keall, S.N., 1989. Feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island based on niche diversity. *N.Z. Journal of Zoology* 16: 269.

Castanet, J., Newman, D.G., and Saint Girons, H., 1988. Skeletochronological data on the growth, age, and population structure of the tuatara, *Sphenodon punctatus*, on Stephens and Lady Alice Islands, New Zealand. *Herpetologica* 44: 25–37.

Caughley, G., 1977. *Analysis of Vertebrate Populations*. John Wiley & Sons, London.

Cree, A., and Daugherty, C.H., 1990. Tuatara sheds its fossil image. New Scientist #1739: 22–26.

Crook, I.G., 1975. The tuatara. *In* G. Kuschel (Ed): *Biogeography and Ecology in New Zealand*, pp. 331–352. Junk, The Hague.

Daugherty, C.H., Cree, A., Hay, J.M., and Thompson, M.B., 1990. Neglected taxonomy and continuing extinctions of tuatara (*Sphenodon*). Nature 347: 177–179.

Dawbin, W.H., 1982a. The tuatara *Sphenodon punctatus*: aspects of life history, growth and longevity. *In* D.G. Newman (Ed): *New Zealand Herpetology*, pp. 237–250. New Zealand Wildlife Service Occasional Publication Number 2.

———— 1982b. The tuatara *Sphenodon punctatus* (Reptilia: Rhynchocephalia): a review. *In*: D.G. Newman (Ed): *New Zealand Herpetology* pp. 149–181. New Zealand Wildlife Service Occasional Publication Number 2.

Gans, C., 1983. Is *Sphenodon punctatus* a maladapted relict? *In* A.G.J. Rhodin, and K. Miyata (Eds): *Advances in Herpetology and Evolutionary Biology: Essays in Honor of Ernst E. Williams*, pp. 613–620. Museum of Comparative Zoology, Cambridge, Massachusetts.

Meads, M., 1982. [Comment in Discussion following article by R.E. Barwick.] *In* D.G. Newman (Ed): *New Zealand Herpetology*, p. 393. New Zealand Wildlife Service Occasional Publication Number 2.

Moller, H., 1985. Tree wetas (*Hemideina crassicruris*) (Orthoptera: Stenopelmatidae) of Stephens Island, Cook Strait. *N.Z. Journal of Zoology* 12: 55–69.

Newman, D.G., 1982. Current distribution of the tuatara, *Sphenodon punctatus*. *In* D.G. Newman (Ed): *New Zealand Herpetology*, pp. 145–147. New Zealand Wildlife Service Occasional Publication Number 2.

———— 1986. Can tuatara and mice co-exist? The status of the tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia), on the Whangamata Islands. *In*: *The Offshore Islands of Northern New Zealand*. New Zealand Department of Lands and Survey Information Series 16: 179–185.

———— 1987. Burrow use and population densities of tuatara (*Sphenodon punctatus*) and how they are influenced by fairy prions (*Pachyptila turtur*) on Stephens Island, New Zealand. *Herpetologica* 43: 336–344.

Pickard, C.R., and Towns, D.R., 1988. Atlas of the Amphibians and Reptiles of New Zealand. *Conservation Sciences Publication* 1. New Zealand Department of Conservation, Wellington.

Saint Girons, H., 1980. Thermoregulation in reptiles with special reference to the tuatara and its ecophysiology. *Tuatara* 24: 59–80.

Schmidt, G., and Inger, R., 1957. *Living Reptiles of the World*. Hamish Hamilton, London.

Sokal, R.R., and Rohlf, F.J., 1981. *Biometry* (2nd ed). Freeman, New York.

Walls, G.Y., 1978. The influence of the tuatara on fairy prion breeding on Stephens Island, Cook Strait. *N.Z. Journal of Ecology* 1: 91–98.

——— 1981. Feeding ecology of the tuatara (*Sphenodon punctatus*) on Stephens Island, Cook Strait. *N.Z. Journal of Ecology* 4: 89–97.

Received 23 May 1990; accepted 3 December 1991

© Journal of the Royal Society of New Zealand,
Volume 22, Number 2, June 1992, pp 131-152

A comparison of Jurassic marine benthonic faunas from South America and New Zealand

S. E. Damborenea* and M. O. Manceñido*

A direct comparison of Jurassic marine bivalves and brachiopods from the Murihiku terrane of New Zealand and the Argentinian-Chilean basins indicates that faunal links between equivalent facies settings of the two regions were even stronger than previously acknowledged. Some faunal elements usually regarded as Maorian endemics are also present in South America, particularly during the Early Jurassic (Aratauran and Ururoan). Middle Jurassic (Temaikan) inoceramid sequences share key elements, probably forming a latitudinally distinct stock. Two successive *Retroceramus* lineages that repeat general morphological trends are now recognized in South American and New Zealand Middle and Late Jurassic deposits, providing new data on correlation at the Temaikan – Heterian boundary. Since the New Zealand local stage system was based mostly on bivalves, as ammonite faunas are sparse, information from accurately dated Argentinian faunas will help improve correlation with the International Standard. From a paleogeographical point of view, the remarkable degree of faunal exchange suggests the existence of suitable neritic habitats along the margins of Gondwana and is also relevant to the issue of the provenance of New Zealand terranes.

Keywords: Palaeozoology, bivalves, brachiopods, Murihiku terrane, Andes, Early Jurassic (Aratauran, Ururoan), Middle Jurassic (Temaikan), Retroceramus, *New Zealand, Argentina, Chile, palaeogeography, Gondwanaland*

INTRODUCTION

There has been considerable debate about the configuration of crustal blocks along the southern rim of the Mesozoic Pacific and the provenance of the pre-Cretaceous terranes that make up modern New Zealand (Howell, 1980; Bishop *et al.*, 1985; Hallam, 1986; Bradshaw, 1989). An important line of evidence for paleogeographic relationships is the composition of shallow water marine invertebrate faunas. Although South American and New Zealand Jurassic benthonic faunas have often been considered in global paleogeographic syntheses (Hallam, 1977, 1986; Hölder, 1979; Stevens, 1980, 1990; Ager, 1986; Crame, 1986, 1987; Ager and Sun, 1988), the faunas have never been compared in detail by someone with direct knowledge of both regions, so important similarities have been missed. This paper reports the first direct comparison of Jurassic marine invertebrate faunas from the Murihiku terrane of New Zealand and the Argentinian – Chilean basins of South America.

This review is based on examination of collections housed at Otago University (OU) and Auckland University (AU) and additional materials held at Lower Hutt (New Zealand Geological Survey, NZGS) and Christchurch (Canterbury Museum), supplemented by field work in the North and South Islands. South American material referred to is mostly held at La Plata Natural Sciences Museum (MLP), but representative casts and molds, including some of the figured specimens, have been deposited in AU (bivalves) and OU (brachiopods).

Jurassic bivalves from New Zealand are relatively well-known, brachiopods less so (Trechmann, 1923; Marwick, 1953b; Speden, 1970; Fleming, 1987), although there are no recent systematic revisions and some information is available only in unpublished theses

---

* Invertebrate Paleozoology Division, Natural Sciences Museum, Paseo del Bosque, 1900 La Plata, Argentina

(Hudson, 1983; Braithwaite, 1984; MacFarlan, 1985). South American bivalve and brachiopod faunas are now being systematically revised by us and some results have already been published (Damborenea, 1987a, 1987b, 1989, 1990; Manceñido, 1981, 1983). However, much remains unpublished by the authors (Damborenea 1982, 1991; Manceñido, 1978) or has appeared only in preliminary reports (in Riccardi *et al.*, 1988, 1990a, 1990b, 1991; Damborenea, in press a, b; Manceñido and Damborenea, 1990; Manceñido, 1990; Manceñido and Dagys, in press).

FAUNAL COMPARISON THROUGH TIME

A direct correlation between the New Zealand and the South American Jurassic has never been attempted. Instead, the stratigraphy in each region has been related independently to the European Standard Zonation, with differing degrees of accuracy, and so presently available correlations suffer from the accumulated distortions introduced at each step. In this contribution we have adopted the Global Stratigraphic Chart published by Cowie and Bassett (1989). Knowledge of the ammonite faunas in Argentina allows a direct correlation with the Standard Zones (Riccardi, 1984; Riccardi *et al.*, 1988, 1990c). Unfortunately, this is not the case in New Zealand. Nevertheless, the New Zealand ammonite fauna is rich and diverse, and its systematic study will certainly allow a more accurate stage by stage comparison of the two regions in the future. Correlation of the New Zealand Jurassic with the international zonation is possible only at some isolated horizons and therefore a local system of stages has been developed (Marwick, 1953b; Carter, 1974; Stevens and Speden, 1978). We believe that the correlation of the local stages could be improved by reference to the distribution in South America of some of the bivalve groups discussed below (see Table 1).

The following stage by stage comparison must be regarded as preliminary, particularly concerning the ranges in New Zealand of the species considered. Several examples of apparently displaced vertical ranges between the two regions have been detected. Further work is necessary to interpret their significance because the stratigraphic framework is not sufficiently well-known.

HETTANGIAN – SINEMURIAN (EARLY ARATAURAN)

Several elements of Lower Aratauran bivalve faunas from New Zealand are present in the Andes, or are represented in both regions by very closely related forms. They include the following:

Palmoxytoma (Pl. 1, Fig. 1)

When first described (Cox, 1961), *Palmoxytoma* was thought to be restricted to Europe, but it was already known (as *Oxytoma*) or was later reported from many other Boreal-Pacific areas, such as Canada (Frebold, 1957, 1966), Japan (Hayami, 1959, 1975) and Siberia (Polubotko, 1968b). An early record of material from New Zealand, originally referred to as *Oxytoma* sp. by Trechmann (1923) and later to the type species of *Palmoxytoma* by Arkell (1956), seems to have been overlooked by later authors analyzing the paleogeographic distribution of Jurassic bivalves (Hallam, 1977, 1983; Hölder, 1979), and so *Palmoxytoma* has been cited as typically Boreal. Although this seems to be the case for later Sinemurian and Pliensbachian times, both the New Zealand and the Argentinian records show that during the Hettangian-earliest Sinemurian its distribution included the southern circum-Pacific. Although scarce, Argentinian specimens of *Palmoxytoma* sp. have been figured (Riccardi *et al.*, 1988, 1991; Damborenea, in press a; Pl. 1, Fig. 1a here). They appear more similar to coeval New Zealand specimens from the South Island Aratauran (Pl. 1, Fig. 1b) than to Boreal forms. The New Zealand species has yet to be formally described, despite the fact that it seems to be relatively abundant at certain levels, such as the Psiloceras beds of the Hokonui Hills (several specimens seen at OU, also personally collected at Otapiri Stream). Most of the New Zealand material has been labelled and listed as *Oxytoma* sp. in the past and so remained unrecognized.

In Argentina *Palmoxytoma* is found in the upper Hettangian of southern Mendoza Province, associated with ammonites of the Waehneroceras – Schlotheimia and Badouxia canadensis Ammonite Zones (Riccardi *et al.*, 1988, 1991).

Otapiria (Pl. 1, Fig. 2)

Early Jurassic *Otapiria* is common and well known both in New Zealand and in Argentina (Stevens and Speden, 1978; Damborenea, 1980). In the Andes the genus is represented by two species with different biostratigraphic ranges: the older is *O. pacifica* Covacevich and Escobar (1979) from the latest Hettangian to the early Sinemurian (Pl. 1, Fig. 2a; see also Riccardi *et al.*, 1988, 1991). This species gives its name to a bivalve Assemblage Zone (Damborenea in Riccardi *et al.*, 1990a).

As it has a finely ribbed right valve and an almost smooth left valve, *Otapiria pacifica* is very similar to, or may be even conspecific with, *O. limaeformis* (Zakharov) from northeastern USSR (Zakharov, 1962; Polubotko, 1968b). It is therefore quite different from coeval *O. marshalli* from New Zealand, yet somewhat reminiscent of latest Triassic (Otapirian) *O. dissimilis* Marwick and of early Aratauran forms from the North Island traditionally identified as *O. marshalli* (Pl. 1, Fig. 2b).

Finely ribbed *Chlamys*

Both in New Zealand and the Andes a species of finely ribbed *Chlamys* is found in the Hettangian – Early Sinemurian. This non lamellose species is allied to the group of *Chlamys valoniensis* (Defrance) (Damborenea, 1991).

LATE SINEMURIAN – EARLY PLIENSBACHIAN (LATE ARATAURAN)

In addition to having a number of bivalves in common, similarities between New Zealand and Andean brachiopods are apparent during this interval (see below).

Otapiria (Pl. 1, Fig. 3)

The species *O. neuquensis* Damborenea (1987b), Pl. 1, Fig. 3a, is very close to the typical Aratauran *O. marshalli* Trechmann (1923), Pl. 1, Fig. 3b, but Andean specimens are consistently smaller in size and, although they appear in similar facies settings, they are never so abundant as in New Zealand – New Caledonia. This species was initially known only from southern Neuquén, but it was later also found in southern Mendoza Province. Its stratigraphic range is from the latest Sinemurian to the earliest Pliensbachian in Argentina (uppermost Miltoceras to Dubariceras Ammonite Zones, Riccardi *et al.*, 1988, 1991) and it gives its name to a bivalve Assemblage Zone (Damborenea in Riccardi *et al.*, 1990a). In New Zealand *Otapiria marshalli* is used as an index fossil for the Aratauran Stage in the North Island, where ammonites are uncommon. At the type locality in the Hokonui Hills *O. marshalli* does not appear with the earliest Jurassic ammonites but a few metres above them.

Kalentera (Pl. 1, Fig. 4)

Since its initial description (Marwick, 1953b) this peculiar bivalve genus has been regarded as an endemic Maorian taxon (Grant-Mackie, 1960; Hallam, 1977; Stevens and Speden, 1978; etc.), known only from the Late Triassic and Early Jurassic rocks of New Zealand – New Caledonia.

The discovery of material clearly belonging to *Kalentera* in Lower Jurassic sediments of western Argentina (Damborenea, in press a, c; in Riccardi *et al.*, 1991), Pl. 1, Fig. 4a, is therefore of great paleobiogeographic interest. By Early Jurassic times this group of bivalves seems to have been restricted to the South Pacific. The Argentine specimens are very close to *K. mackayi* Marwick (Pl. 1, Fig. 4b), with only minor differences in shell proportions. The faunal association and inferred paleoenvironment of Argentinian localities correspond exactly with those recorded in New Zealand. Shell morphology suggests a superficial infaunal mode of life for *Kalentera* species. Type and stability of substrate seem to have been significant factors controlling their distribution. As in New Zealand, the associated fauna is dominated by shallow burrowers and epifaunal bivalves, such as *Grammatodon costulatus* (Leanza), *Otapiria neuquensis* Damborenea, *Palaeonucula* n. sp., pectinids, limids and ammonoids. Grant-Mackie (1960) envisaged a "relatively flat area of the sublittoral zone of the continental shelf with fairly uniform bottom conditions", as a likely environment.

Minetrigoniidae (Pl. 1, Fig. 5)

This trigoniacean family was very diverse in the Triassic of the Pacific-Arctic region, but apparently disappeared from New Zealand at the end of the Triassic (Fleming, 1987). Some forms, probably representing descendants of Pacific Triassic stocks such as *Maoritrigonia* (Pl. 1, Fig. 5b) and referred to the genus *Myophorigonia*, are known from the Early Jurassic of the Argentinian and Chilean Andes (Groeber, 1924; Levy, 1967; Pérez and Reyes, 1977; Damborenea, in press a), Pl. 1, Fig. 5a. The fact that most of the abundant and varied Early Jurassic trigoniacean fauna of the Andes is restricted to littoral and sublittoral environments, with medium to coarse-grained sediments, may explain the absence (or extreme scarcity) of trigoniaceans in the New Zealand Early Jurassic. The appropriate facies is not preserved in New Zealand rocks dating from that time. This interpretation is an alternative to the mass extinction explanation proposed by Fleming (1964 :200; 1987 :16).

Minetrigoniidae from the Andes extend at least from late Sinemurian to late Pliensbachian times, represented by *"Myophorigonia" neuquensis* (Groeber) and its allies. The group is now under revision (Pérez and Damborenea, in preparation).

Plate 1 – Some of the Late Triassic – Early Jurassic bivalves from New Zealand and Argentina which show close relationships. **a**: Argentinian specimens; **b**: New Zealand specimens. More details given in text. All specimens × 1 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.

1.– *Palmoxytoma* sp.; 1a: MLP 22253, Arroyo Malo, Rio Atuel area, Mendoza Province (M1394), Hettangian; 1b: OU 17810 (2), junction of Otapiri Stream and Taylors Creek, Hokonui Hills, (S169/f455, coll. Grebneff), Aratauran.

2.– 2a: *Otapiria pacifica* Covacevich y Escobar, MLP 22261, Arroyo Malo, Rio Atuel area, Mendoza Province (M1722), Sinemurian; 2b: *Otapiria* cf. *marshalli* (Trechmann), MLP 24871, N of Arataura Point, south Kawhia coast (R15/f8587), Aratauran.

3.– 3a: *Otapiria neuquensis* Damborenea, MLP 19997, Puesto Araya, Rio Atuel, Mendoza Province (M352), lower Pliensbachian;

3b: *Otapiria marshalli* (Trechmann), MLP 24872, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

4.– 4a: *Kalentera* n. sp. Damborenea, MLP 24294 (1), composite mold, Arroyo Las Chilcas, Rio Atuel area, Mendoza Province (M1423), lower Pliensbachian; 4b: *Kalentera mackayi* Marwick, MLP 24873, internal mold, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

5.– 5a: *"Myophorigonia" neuquensis* (Groeber), MLP 24324 (1) (holotype), Puruvé Pehuén, upper Catan Lil river, Neuquén Province (coll. P. Groeber), Pliensbachian; 5b: *Maoritrigonia* sp., AU 576 = L 3829, external mold, S of Arataura Point, south Kawhia coast (R15/f8833, coll. Claridge), Otapirian.

6.– *"Camptochlamys" wunschae* (Marwick); latex casts.; 6a: MLP 23658 (1), Arroyo Ñireco, Neuquén Province (M1362), Pliensbachian; 6b: NZGS TM 2406 (2) (holotype), Wyndham Rapids, Southland (S178/f490, coll. P. Wunsch), Ururoan.

7.– 7a: *Plicatula (Harpax) rapa* Bayle & Coquand, MLP 19643, X2, Arroyo Serrucho, Mendoza Province (M1316); MLP 20687-a, Arroyo Ñireco, Neuquén Province (M1362), Pliensbachian;

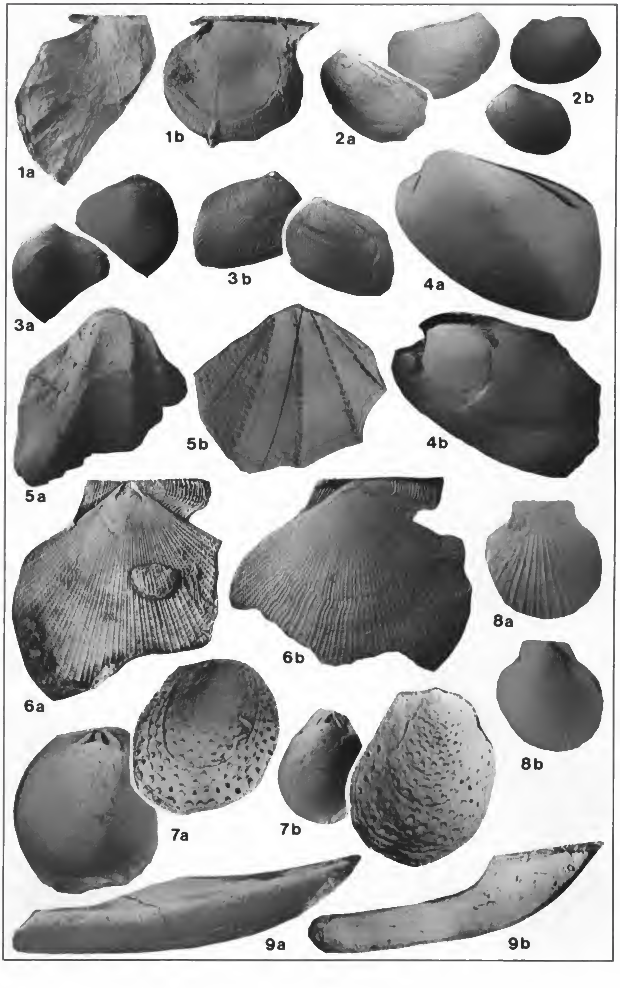
7b: *Plicatula (Harpax)* cf. *rapa* Bayle & Coquand, OU 14943 and 14947, X2; internal and external molds, Heale Ridge, right slope of Otapiri Valley (E49, coll. D. MacFarlan), Ururoan.

8.– 8a: *Kolymonectes coloradoensis* (Weaver), MLP 23686 (1), Cerro Roth, Piedra Pintada, Neuquén Province (M112), Pliensbachian; 8b: *Kolymonectes* ? sp., OU 14289, Conical Hill, left slope of Otapiri Valley (S169/f860, coll. D. MacFarlan), Ururoan; internal molds.

9.– *Gervillia (Cultriopsis)* sp., 9a: MLP 16386, × 2, Cerro Roth, Piedra Pintada, Neuquén Province (M104), Pliensbachian; 9b: OU 14942, Heale Ridge, right slope of Otapiri Valley (E49, coll. D. MacFarlan), Ururoan; internal molds.

(1) Casts at AU also.

(2) Casts at MLP also.


1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b
7a
7b
8a
8b
9a
9b

"Spiriferina" ongleyi Marwick (Pl. 2, Fig. 1–3)

Andean material from late Sinemurian beds of western Argentina (Manceñido, 1990; Riccardi *et al.*, 1991) most closely resembles this characteristic species of the Aratauran of the South Island (Marwick, 1953b). A redescription of the New Zealand form is being jointly undertaken with Prof. J.D. Campbell. It has been suggested by Wright and Campbell (1990) that Marwick's species may have evolved from the Otapirian (Rhaetian) *Mentzelia kawhiana* (Trechmann, 1923), the two representing a single lineage.

Furcirhynchia (Pl. 2, Fig. 4–5)

This genus is widespread although sporadic in early Jurassic deposits throughout Europe, western North America, Japan, Indonesia, New Zealand (Trechmann, 1923; MacFarlan, 1985, 1990; Ager and Sun, 1988) and Argentina (Manceñido, 1978, 1990, in Manceñido and Dagys, in press). Earliest occurrences in the lower Aratauran (probably as old as Hettangian) of the Otapiri valley are followed in New Zealand by records up into the upper Ururoan (Toarcian) of the Kawhia syncline and include two successive different species. The Argentinian early Pliensbachian material identified as *Furcirhynchia* sp. (Pl. 2, Fig. 4a) is broad and depressed and more akin to the Aratauran species (Pl. 2, Fig. 4b) than to the more everted Ururoan one (Pl. 2, Fig. 5b).

PLIENSBACHIAN (EARLY URUROAN)

This time interval is marked by an apparent increase in the similarity between South American and New Zealand faunas, and the pre-*Dactylioceras* Ururoan bivalve and brachiopod faunas of the two regions have several elements in common. However, the diagnostic Ururoan bivalve *Pseudaucella marshalli* (Trechmann) appears to be absent from the Andes. Conversely, one of the commonest Pliensbachian Andean pectinaceans, presently referred to *Kolymonectes* (Pl. 1, Fig. 8a), may be poorly represented in New Zealand, as limited material is available (Pl. 1, Fig. 8b).

Some faunal associations found in both regions are almost identical to the species level. They include certain pteriaceans, such as *Gervillia (Cultriopsis)* sp. (Pl. 1, Fig. 9), in addition to the taxa discussed below.

Plate 2 – Some of the Lower Jurassic brachiopods from New Zealand and Argentina which show close relationships. **a**: Argentinian specimens; **b**: New Zealand specimens. More details given in text. All specimens × 1.5 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.

1–3.– 1a, 2a, 3a: *"Spiriferina"* cf. *ongleyi* Marwick, MLP 24483 (1), 24482 (1), 24481; Arroyo Las Chilcas, River Atuel area, Mendoza Province (M1419), uppermost Sinemurian;

1b, 2b, 3b: *"Spiriferina" ongleyi* Marwick, MLP 24875, W face of Ben Bolt, opposite Harrington Bridge, Hokonui Hills (JDC4069), Aratauran; MLP 24876, N face of Ben Bolt, Hokonui Hills (S169/f676), upper Aratauran.

4–5.– 4a: *Furcirhynchia* sp., MLP 24415, Roadside to Sañicó, Piedra Pintada area, Neuquén Province (coll. A. Leanza), Pliensbachian;

4b: *Furcirhynchia* sp., MLP 24877, × 2, junction of Otapiri Creek and Taylors Stream, Hokonui Hills (S169/f455), lower Aratauran;

5b: *Furcirhynchia* sp., MLP 24878, × 2, N of Ururoa Point, south Kawhia coast (N73/f5), upper Ururoan.

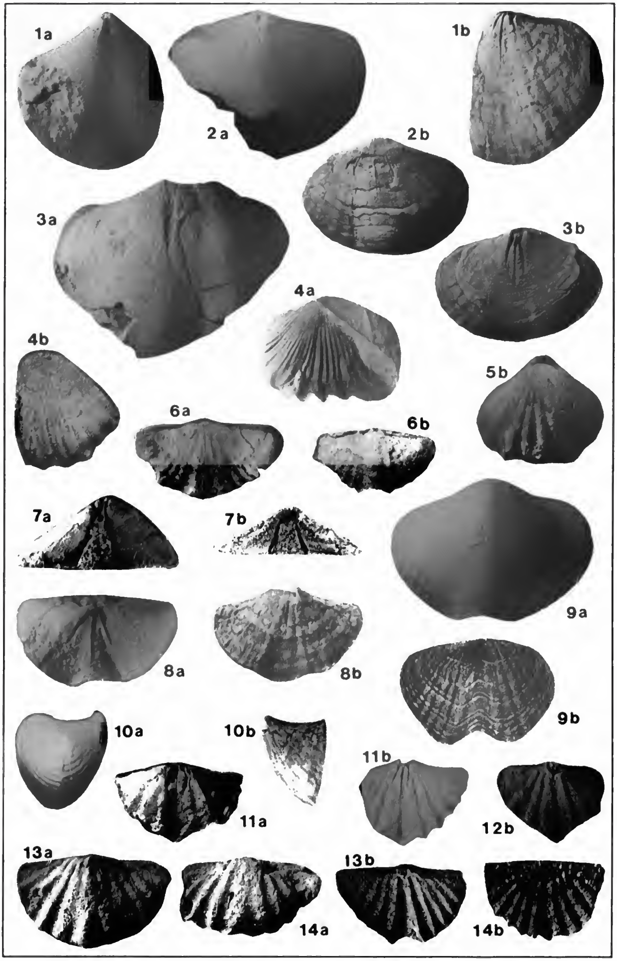
6–10.– 6a, 7a, 8a, 9a, 10a: *"Spiriferina" tumida ericencis* de Greg., MLP 10015-b, 10015-c, Carrin Cura Creek, SW of Bayo Hill, Neuquén Province (coll. G. Parker), Pliensbachian; MLP 15285, Arroyo La Laguna, River Los Patos area (M431), upper Pliensbachian; (10a × 1);

6b, 7b, 8b, 9b, 10b: *"Spiriferina" radiata* Hector, MLP 24879-a, 24880-a, OU C4050', Conical Hill, left slope of Otapiri Valley (S169/f860, coll. J.D. Campbell et al.), lower Ururoan.

11–14.– 11a, 13a, 14a: *"Spiriferina"* cf. *muensteri* (Davidson), MLP 24884, 24882, 24883, 8 km S of Estancia Santa Isabel, Neuquén Province (M1055), upper Pliensbachian; × 2;

11b, 12b, 13b, 14b: *"Spiriferina"* cf. *muensteri* (David.), OU C4040, C4042, C4041, C4051, Conical Hill, left slope of Otapiri Valley (S169/f860, coll. J.D. Campbell), lower Ururoan; × 3.

(1) Casts at OU also.


1a
1b
2a
2b
3a
3b
4a
4b
5b
6a
6b
7a
7b
8a
8b
9a
9b
10a
10b
11a
11b
12b
13a
13b
14a
14b

"Camptochlamys" wunschae (Marwick) (Pl. 1, Fig. 6)

"Camptochlamys" wunschae (Marwick, 1953b) belongs to a group of species known from the Upper Triassic to Toarcian of both Boreal and Austral Pacific margins. Upper Triassic forms include *"C". inspecta* Kiparisova (in Kiparisova *et al*., 1966) from Siberia and material from Otapirian and even Otamitan of New Zealand (OU collections). During the Pliensbachian this group includes *"C". wunschae* (Marwick, 1953b) in New Zealand (Pl. 1, Fig. 6b) and Argentina (Damborenea, in press a, b; see Pl. 1, Fig. 6a here) and *"C". proprius* Milova (1976) in Siberia.

It is a fairly homogeneous group, but its systematic relationships are still unclear. Although it is currently referred to *Camptochlamys*, it is distinct enough to justify the erection of a new genus (Damborenea, in press b). Reference to *Camptochlamys* obscures its real relationships, giving rise to the view proposed by Marwick (1953a) that this is a typical Tethyan element of the New Zealand fauna.

Specimens from the Andes had been referred to *Pecten* or *Chlamys* in the past and so their true relationships were not realised. *"Camptochlamys" wunschae* is known in Argentina from southern Mendoza to southern Neuquén (and probably Rio Negro) Provinces and ranges in age from mid to late Pliensbachian. It is found only in very fine-grained sediments, from marls to tuffaceous siltstones, but never in laminated dark shales. This species is locally abundant rather than widespread and seems to have been limited to very low energy but well-oxygenated environments. It is generally associated with a variety of limid species, commonly with sponge spicules but never with corals or thick-shelled epifaunal bivalves. *"Camptochlamys" wunschae* was a byssally attached pectinid and sponges could have provided a suitable substrate. The left valve often bears epizoans (such as plicatulids, small oysters and serpulids) on its external surface.

Plicatula (Harpax) rapa Bayle and Coquand (Pl. 1, Fig. 7)

Within the cosmopolitan genus *Plicatula* several groups of species can be recognized. Here we refer this group to the subgenus *Harpax* which shows many shell features that distinguish it from *Plicatula* s.s. (Damborenea, 1982, 1991). The two taxa (*Plicatula* and *Harpax*) coexisted during the early Jurassic, but whilst *Harpax*, known from the Triassic and early Jurassic, seems to have dissappeared shortly afterwards, *Plicatula* s.s. has persisted to the present.

Within *Harpax* there is a group of late Triassic – early Jurassic species distributed in both Boreal and Austral regions of the Pacific (Damborenea, in press b). The group includes *P.(H.) kolymica* Polubotko (in Kiparisova *et al*., 1966; Polubotko, 1968a; Bychkov *et al*., 1976) from the Triassic of Siberia. Pliensbachian forms comprise *P. (H.) rapa* Bayle and Coquand (1851) from Argentina (Pl. 1, Fig. 7a) and Chile, *P. (H.)* cf. *rapa* from New Zealand (Pl. 1, Fig. 7b) and *"H. spinosus* (Sow.)" in papers by Polubotko (1968b) and Sey (1984). *P. (H.) rapa* is widespread in Argentina, ranging in age through most of the Pliensbachian, reaching probably the earliest Toarcian.

Juvenile specimens of *P. rapa* have been observed cemented to the outer surface of other shells, mostly *"Camptochlamys" wunschae* and some left valves of *P. rapa* show xenomorphic sculpture (Pl. 1, Fig. 6a). The abundance of isolated and unattached right valves suggests that this bivalve changed to a reclining mode of life during ontogeny, probably due to loss or destruction of the substrate shell. The range of sediment types in which this is known to occur in Argentina is quite similar to that of *"C." wunschae*, but *P. rapa* seems to be more widespread.

The identity of the material from New Zealand is still in doubt pending revision, but it appears that specimens formerly identified merely as *Plicatula* sp. belong to the same group of species and may be conspecific. Not only is the morphological similarity great, but also its frequent association with *"C". wunschae* is strikingly alike.

Limidae

Both in the Hokonui Hills and in several Andean localities, an assemblage dominated by limids developed during the Pliensbachian. In both areas very similar species of *Antiquilima*, *Pseudolimea* and *Plagiostoma* may be found in association with *"Camptochlamys" wunschae* and *Plicatula (Harpax) rapa.* A recent revision of this group is available (although not published) for New Zealand (Braithwaite, 1984). In contrast, large thick-shelled species of *Ctenostreon* are conspicuous elements of shallow water faunas in the Andes. The absence of *Ctenostreon* in New Zealand may be accounted for by the lack of appropriate facies.

"Spiriferina" tumida – radiata plexus (Pl. 2, Fig. 6–10)

"Spiriferina" radiata Hector has not been studied in sufficient detail and only the morphology of its pedicle valve has been illustrated. It is a conspicuous element of New Zealand Ururoan assemblages, as indicated by collections held at OU, NZGS, AU and additional re-sampling (*cf.* also Trechmann, 1923; Marwick, 1953b; and Pl. 2, Fig. 6b–10b).

Similar material is known from Late Pliensbachian deposits of western Argentina, where it has been considered to differ subspecifically from *S. tumida* (von Buch) (*cf.* Manceñido 1978, 1981, 1990; Manceñido and Dagys, in press; and Pl. 2, Fig. 6a–10a), but accurate determination awaits the completion of current revision.

"Spiriferina" cf. *muensteri* (Davidson) (Pl. 2, Fig. 11–14)

In New Zealand, *"Spiriferina" radiata* is sometimes accompanied by a small but unmistakeable, strongly plicate spiriferinacean which is very rare and still undescribed. During this project, re-collection made with Prof. J.D. Campbell has substantially increased the amount of material from earliest Ururoan of the Hokonui Hills and we are now able to make comparisons with our abundant material of a larger size range from the Late Pliensbachian of western Argentina. *"Spiriferina" muensteri* from the Lower Jurassic of central Chile was mentioned but not figured at the end of the last century by Moericke (1894) and recently also by Ager (1986).

TOARCIAN (LATE URUROAN)

In late Ururoan times, a number of New Zealand brachiopods (including some rhynchonellides and the last spiriferinaceans from the *Dactylioceras* beds) point to much stronger relationships with core Tethyan elements than with Andean ones and the probable connection was via Indonesia (*cf.* Manceñido, in press; Manceñido and Dagys, in press). Although typical elements of the Andean bivalve faunas, such as *Posidonotis cancellata* (Leanza) appear to be absent, some bivalves are still common to both, mostly belonging to cosmopolitan genera such as *Entolium, Oxytoma, Chlamys, Pseudolimea, Pleuromya.*

AALENIAN (LATEST URUROAN ?, EARLIEST TEMAIKAN ?)

Meleagrinella (Pl. 3, Fig. 1)

Meleagrinella beds are a common feature both in the Andes and in New Zealand, as in other parts of the world. In both areas the European species *Meleagrinella echinata* (W. Smith) has been cited, but they are less similar to that than to each other.

For many decades, the incoming of *Meleagrinella* (Pl. 3, Fig. 1a) was thought to mark the base of the Aalenian deposits in the Andes (Weaver, 1931). However, recent studies show that the first appearance of this genus marks the base of one of the sedimentary cycles recognized in the area, varying in age from Toarcian to Aalenian or even Bajocian in different localities and usually associated with coarse calcareous sandstone beds (Damborenea, 1991).

In New Zealand, the incoming of *Meleagrinella* (Pl. 3, Fig. 1b) has been used to mark the base of the Temaikan local stage (Marwick, 1953b). However, Hudson (1983) regards that usage as unsuitable because its incoming is controlled by facies change.

BAJOCIAN (EARLY TEMAIKAN)

Several elements of the rich Bajocian bivalve fauna from the Andes closely resemble

Temaikan bivalves. Most of them belong to cosmopolitan groups (*Camptonectes* s.s., *Vaugonia, Pleuromya, Myophorella,* etc.) but a few are distinctive enough to be commented upon here.

Propeamussium (Pl. 3, Fig. 2)

A group of species of *Propeamussium*, characterized by small size and strong external ribbing of the left valve, is known from several places, including the Andes and New Zealand. In both regions they have been thought to differ sufficiently from other *Propeamussium* to be described as distinct species, and have been called *Variamussium clamosseum* Marwick (1953b) in New Zealand (Pl. 3, Fig. 2b) and *Pecten andium* Tornquist (1898) in Argentina (Pl. 3, Fig. 2a). Also similar is *P. geelvinki* Skwarko (1974) from the Lower Bajocian of western Australia. A *Propeamussium andium* bivalve Assemblage Zone has been proposed (Damborenea, in press c) for the Andean Bajocian, whereas *P. clamosseum* seems to have a longer vertical range, reaching the upper Temaikan in New Zealand (*cf.* Westermann and Hudson, 1991).

Retroceramus (Pl. 3, Fig. 3, 4)

The succession and distribution of Middle Jurassic inoceramid species in New Zealand are complex, and understanding them has been inhibited by several problems, such as the poor preservation of most of the material, inadequate knowledge of their intraspecific variation and the occurrence of intermediate forms. Associated ammonites are scarce and yet to be adequately described. By far the most accurately dated succession of Middle Jurassic inoceramid species in the southern Hemisphere is that from Argentina, where the succession has a well studied ammonite zonation (see Riccardi *et al.*, 1990c). Argentina can therefore assist in understanding other regions (Damborenea, 1990) such as New Zealand, since the Andean and New Zealand successions have some *Retroceramus* species in common.

Plate 3 – Some of the Middle Jurassic bivalves from New Zealand and Argentina which show close relationships. a: Argentinian specimens; b: New Zealand specimens. More details given in text. All specimens × 1 and collected by the authors, except where otherwise indicated. Locality number data between parentheses.

1.– *Meleagrinella* cf. *echinata* (Smith); 1a: MLP 24874, Bardas Blancas, Mendoza Province (M289), Aalenian;

1b: AU 9228 = L 3830, Pomarangei Road, Herangi Range, (R16/f115, coll. N. Hudson), Temaikan.

2.– 2a: *Propeamussium andium* (Tornquist), MLP 24323, × 2, Carro Quebrado, Neuquén Province (M 154), Bajocian;

2b: *Propeamussium clamosseum* (Marwick), AU 11429 =L 3831, × 2, Te Whakapatiki Stream, above junction with Awakino river, Mahoenui (R17/f566, coll. N. Hudson), upper Temaikan.

3.– 3a: *Retroceramus* aff. *inconditus* (Marwick), MLP 23375, Aguada de la Mula, Sierra de Reyes, Mendoza Province (M218), Bajocian;

3b: *Retroceramus inconditus* (Marwick), OU 16404, Lindem Hills Quarry, Marokopa Valley (coll. D. MacFarlan), Temaikan.

4.– 4a: *Retroceramus* cf. *marwicki* (Speden), MLP 23372, Chacay Melehue, Neuquén Province (M1496), upper Bajocian;

4b: *Retroceramus marwicki* (Speden), AU 12155, Opouatia Cliff, Port Waikato area (R13/f213, coll. J. Grant-Mackie & G. Westermann), Temaikan.

5.– 5a: *Retroceramus patagonicus* (Philippi), MLP 23384 (1), Chacay Melehue, Neuquén Province (M1507), upper Bathonian;

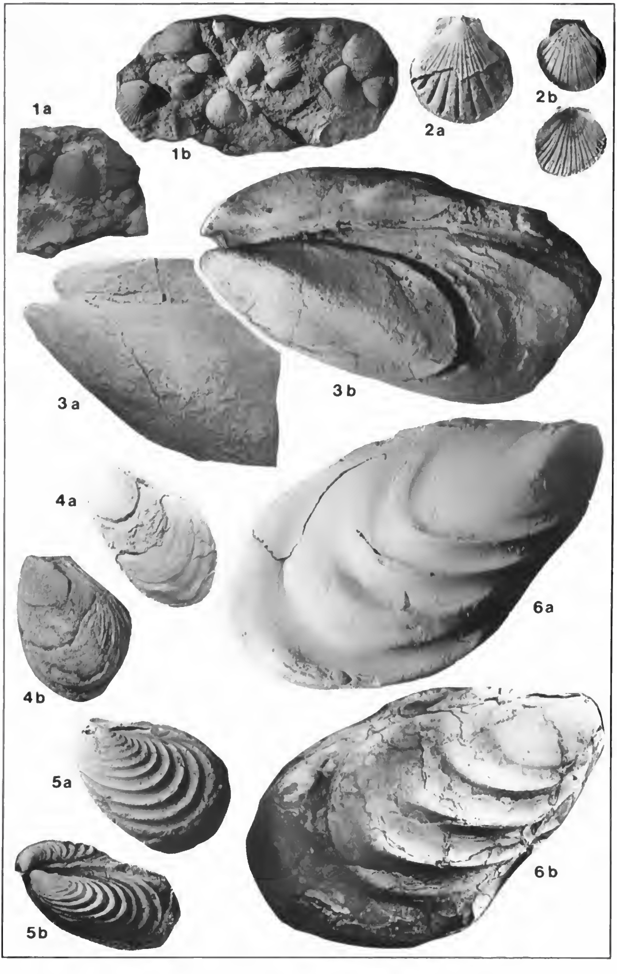
5b: *Retroceramus* cf. *patagonicus* (Philippi), AU 11583 = L 3828, SE end of Oraka Bay, Totara Peninsula, Kawhia Harbour, (R17/f219, coll. N. Hudson et al.), Oraka Sandstone.

6.– *Retroceramus stehni* Damborenea, 6a: CPBA 7392 (original at Buenos Aires University, 1, 2), Chacay Melehue, Neuquén Province (coll. J. Keidel), lower Callovian;

6b: AU 11442 = L 3832, Awakino river, above junction with Te Whakapatiki Stream, Mahoenui (R17/f376, coll. N. Hudson), Kirikiri Group.

(1) Casts at AU also.

(2) Casts at MLP also.


1a
1b
2a
2b
3a
3b
4a
4b
5a
5b
6a
6b

Retroceramus inconditus (Marwick, 1953b) is present in the lower Temaikan of New Zealand (Pl. 3, Fig. 3b), and the poorly known early Bajocian *R.* ? sp. (Damborenea, 1990) from Argentina (Pl. 3, Fig. 3a) is closely related. They are followed by *Retroceramus marwicki* (Speden, 1970) in both regions. This easily recognizable species is found abundantly in upper Temaikan beds of the South and North Islands (Pl. 3, Fig. 4b). Although the Argentinian specimens were referred to as *R.* cf. *marwicki* (Damborenea, 1990; see also Pl. 3, Fig. 4a here), we consider, after our examination of material from both regions, synonymy of the two forms to be almost certain. In the Andes this species was found in upper Bajocian beds of the Rotundum Ammonite Zone, below the incoming of *Retroceramus patagonicus* (Philippi) and characterizes a bivalve Assemblage Zone (Damborenea, in press c).

Retroceramus marwicki belongs to the group of *R. lucifer* (Eichwald) which lived during the early Bajocian in Arctic regions (Imlay, 1955; Polubotko, 1968b). This, and the age (also Bajocian) of the material from the Andes, suggest the need to adjust the age of the *marwicki*-bearing Temaikan in New Zealand, which has been referred to the Callovian, or Bathonian - Callovian, on the basis of preliminary ammonite identifications (Stevens and Speden, 1978).

BATHONIAN – CALLOVIAN (LATE TEMAIKAN – EARLY HETERIAN ?)

Retroceramus (Pl. 3, Fig. 5, 6)

The recent description (Damborenea, 1990) of a Bathonian – Callovian lineage of *Retroceramus* species from Argentina, which had previously been referred to *R. galoi* (in Stehn, 1923; see also Cox *et al*., 1969), may help us to understand similar forms from New Zealand which had either been likewise referred to *R. galoi* or had remained undescribed. The presence of strongly folded *Retroceramus* below typical *R. galoi* was recognized by Hudson (1983: 83–86; see also Westermann and Hudson, 1991: 690). The identity of these forms is particularly important in New Zealand, since the incoming of *R. galoi* marks the base of the Heterian local stage.

The description of *Inoceramus patagonicus* by Philippi (1899) has been overlooked by later authors. The analysis of topotypic material shows that this is a distinct taxon (Damborenea, 1990), characterized by only slightly prosogyrous umbones, long ligamental area and ornamented by regularly spaced, narrow concentric folds separated by intervals up to twice as wide (Pl. 3, Fig. 5a). The Argentinian specimens are associated with a rich ammonite fauna of the Steinmanni Zone and the *Retroceramus patagonicus* bivalve Assemblage Zone (Damborenea, in press c) is thus late Bathonian in age. Some New Zealand specimens collected by N. Hudson (Pl. 3, Fig. 5b) from localities of the Waikato, Kawhia and Awakino areas (*cf.* Westermann and Hudson, 1991) do seem to belong to this group rather than to the younger *R. galoi*. The true identity of this and similar material from New Zealand, such as *Inoceramus* n. sp. from Loc. 613 in Purser (1961: 28), is vital to the understanding of the basic stratigraphy of the region, because if they are referred to *R. galoi* as has been common up to now, the beds should be referred to the Heterian (by definition). On the other hand, if they are referable to *R. patagonicus* as proposed here, the beds would still be included in the Temaikan, since true *R. galoi* only appears much later in the sequence. At the type locality of both stages (Kawhia Harbour), late Temaikan as presently understood is predominantly represented by apparently non-marine deposits, and a very careful reassessment of the stratigraphy of other areas with a more complete marine succession of this age is necessary. For instance, the Awakino area has yielded "*Retroceramus (R.)* n. sp. A aff. *R. galoi*" and recently described ammonites. The latter confirm close "ties to species from the latest Bathonian Steinmanni Standard Zone of the Andean Province" (Westermann and Hudson, 1991).

In the Andes *R. patagonicus* is followed by *Retroceramus stehni* Damborenea (1990), characterized by large shells ornamented by sharp concentric folds which become lower or fade out dorsally (Pl. 3, Fig. 6a). This species (Pl. 3, Fig. 6b) has also been found in New Zealand below the appearance of typical and abundant *R. galoi* by Hudson (1983) and, as

Retroceramus (R.) n. sp. B, has just been mentioned by Westermann and Hudson (1991). In Argentina and Chile the *R. stehni* bivalve Assemblage Zone (Damborenea, in press c) extends from the latest Bathonian (uppermost Gerthi Ammonite Horizon) to the early Callovian (lower Bodenbenderi Ammonite Zone). It is worth pointing out that the accurate dating of "*R.* n. sp. B" from New Zealand (Westermann and Hudson, 1991) seems to be dependent on preliminary determinations of ammonites from the middle Oraka Formation, which deserve further study on more and better preserved material in view of the Callovian age suggested by inoceramids (here) and dinoflagellates (Helby *et al.*, 1988).

There is strong morphological evidence, supported by the stratigraphic distribution of each species, that *R. patagonicus* and *R. stehni* from the Andes belong to a single evolutionary lineage (Damborenea, 1990), equivalent to the clade observed in the group of *R. bulunensis* – *R. vagti* (Koshelkina) during the late Bajocian – Bathonian of Arctic regions (Polubotko and Repin, 1988).

OXFORDIAN – TITHONIAN (HETERIAN – PUAROAN)

Retroceramus (Pl. 4, Fig. 1)

The Oxfordian and Kimmeridgian deposits from the Neuquén Basin in Argentina are generally poorly fossiliferous and in part non-marine. Nevertheless, a species of *Retroceramus* very close to the type specimen of *R. galoi* (Boehm, 1907) has recently been figured (Damborenea, 1990) from probably upper Callovian beds in Neuquén (Pl. 4, Fig. 1a). In the Sula Islands *R. galoi* appears in beds of probable Oxfordian age (Boehm, 1907; Westermann *et al.*, 1978) which overlie a Bathonian – early Callovian ammonite fauna (Westermann and Callomon, 1988). In New Zealand the first appearance of *R. galoi* defines the base of the Heterian Stage, which is traditionally referred to the early Kimmeridgian (see Steven and Speden, 1978). On a regional scale, an inoceramid biozone based on *R. galoi* (Crame, 1982) was referred to the ?Early Kimmeridgian – Tithonian. Some recent authors consider that *R. galoi* could range down into the late Callovian (Grant-Mackie *et al.*, 1986; Hudson *et al.*, 1987; Helby *et al.*, 1988). The issue is further complicated by the confusion between *R. patagonicus* and *R. galoi* (see above) and so needs very careful consideration. Nevertheless, even if the name *R. galoi* is restricted to the forms which appear above *R. stehni*, the base of the Heterian is probably older than Kimmeridgian and could be sited somewhere in Callovian – Oxfordian times. The ammonite fauna which accompanies these inoceramids in New Zealand has not yet been revised, but dinoflagellates of Captain King's Shellbed and Ohineruru Formation indicate at least an Oxfordian age (Helby *et al.*, 1988).

Upper Jurassic deposits are well developed in the Magallanes basin of southern Argentina and Chile and the presence of *R.* cf. *haasti* (Hochstetter) was mentioned by Fuenzalida and Covacevich (1988). This material, seen recently by us in Santiago de Chile, is certainly very similar to large specimens of the New Zealand species and is associated with ammonites of probable Kimmeridgian age. In New Zealand the appearance of *R. haasti* defines the base of the Ohauan local stage, referred to the Tithonian (Stevens and Speden, 1978). Crame (1982) recognized a Kimmeridgian – Early Tithonian *R. haasti* inoceramid biozone of regional significance. A diverse microplankton suite from the Kowhai Point Siltstone suggests a Kimmeridgian age (Helby *et al.*, 1988).

Retroceramus galoi and *R. haasti* are regarded as belonging to the same evolutionary lineage (Fleming and Kear, 1960; Speden, 1970; Spörli and Grant-Mackie, 1976) and the recognition of the base of the Ohauan is sometimes obscured by the presence of intermediate forms which are referred to *R.* cf. *subhaasti* (Wandel).

The material from the Tithonian of the Magallanes Basin figured by Feruglio (1937) as *Inoceramus* cf. *steinmanni* Wilckens was later referred by Crame (1982) to *Retroceramus everesti* (Oppel). Specimens compared with *R. everesti* are known from the Puaroan stage in New Zealand (Marwick, 1953b).

Otapiria (Pl. 4, Fig. 2)

The species *Otapiria masoni* Marwick (1953b) is found in Puaroan beds from the North Island (Pl. 4, Fig. 2b). Feruglio (1937) described a very similar taxon from probably Tithonian deposits in the Magallanes Basin as *Pecten degasperii* (Pl. 4, Fig. 2a). This species may belong to *Otapiria* and is very closely related to the New Zealand *O. masoni*. Also allied to the latter, is a small species of *Otapiria* reported from Tithonian rocks of Alexander Island and South Shetland Islands, in Antarctica (Crame, 1984, 1987).

Buchia

Though less abundant than in Arctic regions, *Buchia* species are a common element of New Zealand upper Jurassic faunas. The correlation of these faunas is not yet resolved, but it is generally agreed that in New Zealand *Buchia* appeared later than in other regions (Li and Grant-Mackie, 1988). The *Buchia* sequence in the Andes has not yet been established.

DISCUSSION

Our results indicate that faunal relationships between the Andean and New Zealand regions throughout the Jurassic were much closer than is usually acknowledged in previous reports, particularly when equivalent paleoenvironmental settings are compared.

A number of distinctive faunal elements that have hitherto been regarded as endemic to New Zealand appear instead to have attained wide distributions. By late Triassic times, conspicuous Maorian brachiopods (such as *Clavigera*) had spread to the Chilean Andes. Other examples are increasingly noticeable in early Jurassic times. This knowledge considerably alters the usual picture of high endemism during that time (Fleming, 1967; Stevens, 1977; Grant-Mackie, 1985) which led to the recognition of a Maorian Province developed in isolation. Instead, our results strengthen the view that the Maorian elements formed part of a persistent Paleoaustral Realm (Fleming, 1979; Stevens, 1980; Damborenea, 1991, in press b). In the Middle and Upper Jurassic, the inoceramid sequences which are presently well-known in Argentina show striking similarities with the New Zealand succession. That there was some similarity was already well known, but this study has provided the details. Our results have wide ramifications, but only those strictly related to paleogeography and biostratigraphy will be summarized below.

Paleogeography

During the Early Jurassic (Aratauran and Ururoan) most of the characteristic taxa of New Zealand faunas have their counterparts in certain open water "outer shelf" facies in the southern Andes (Pl. 1, 2). The other more littoral elements of Andean faunas (such as *Weyla*,

Plate 4 – Some of the Late Jurassic bivalves from New Zealand and Argentina which show close relationships. **a**: Argentinian specimens; **b**: New Zealand specimens. More details given in text.
All specimens × 1 except where otherwise indicated. Locality number data between parentheses.

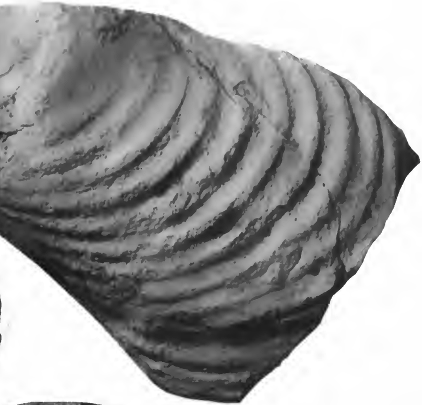
1.– 1a: *Retroceramus* aff. *galoi* (Boehm), MLP 19577, × 0.75, Agua de Reyes, Sierra de Reyes, Mendoza Province (G1213, coll. C. Gulisano), Callovian.

1b: *Retroceramus galoi* (Boehm), OU 14285, E side of Totara Peninsula, Kawhia Harbour (coll. D.S. Coombs), Heterian.

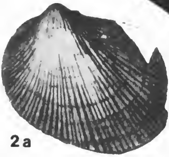
2.– 2a: *Otapiria ? degasperii* (Feruglio), reproduction from Feruglio, 1937, tav. 3, fig. 1 (holotype, at Bologna University, IGPUB 1021), Todos los Santos Hill, Lago Argentino, Santa Cruz Province (coll. E. Feruglio), Tithonian;

2b: *Otapiria masoni* Marwick, NZGS TM 2389 (¹), photograph of plaster cast (holotype), Maretai Stream, Kaawa Road, Waikato Heads, Puaroan (N51/f unregistered, coll. A. Mason).

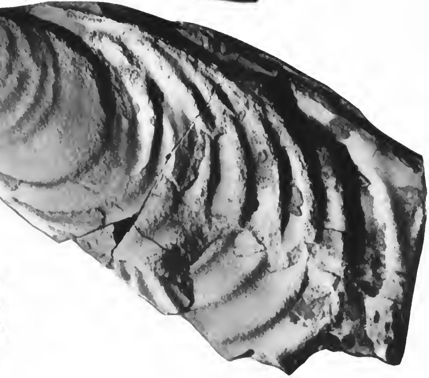
(¹) Casts at MLP also.



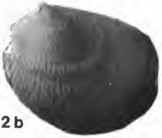
1a



2a



1b



2b

Lopha, Cardinia, Ctenostreon, trigoniids, etc.) are not present in New Zealand and New Caledonia, most probably because these facies are not preserved in the area. The only conspicuous element of New Zealand faunas which has not yet been found in the Andes is *Pseudaucella*, which again is a bivalve whose distribution is controlled by facies. The lack of appropriate environmental settings in New Zealand may also account for some phenomena that have previously been explained in different ways; for example, the apparent absence of trigoniaceans in the Early Jurassic of New Zealand, formerly attributed to extinction, and their sudden reappearance in Middle Jurassic times; or the absence of cardiniids, despite the presence of closely related forms, such as *Torastarte*, in the Triassic of New Zealand.

The observed similarities during the Middle Jurassic include numerous cosmopolitan groups and only the inoceramid sequence has been analyzed in detail here. This shows several elements in common, most of them at the species level. The distribution of this fauna seems to indicate a latitudinally distinct stock (Damborenea, 1990), similar to the upper Jurassic Austral faunas.

The comparison is more difficult for Late Jurassic times because the lithofacies represented in each region are not equivalent. This presumably accounts for: a) the scarcity of Oxfordian and Kimmeridgian inoceramids in the Neuquén Basin; b) the scarcity of buchiids in southern South America.

The similarities between the Jurassic faunas of the Murihiku terrane of New Zealand and those of the Andes may contribute to the discussion on the provenance of that terrane. The striking similarities detected (down to generic and even specific level) involve mainly benthonic organisms (such as bivalves and brachiopods), implying that there were suitable neritic habitats along the margins of Gondwana to allow this remarkable degree of faunal exchange.

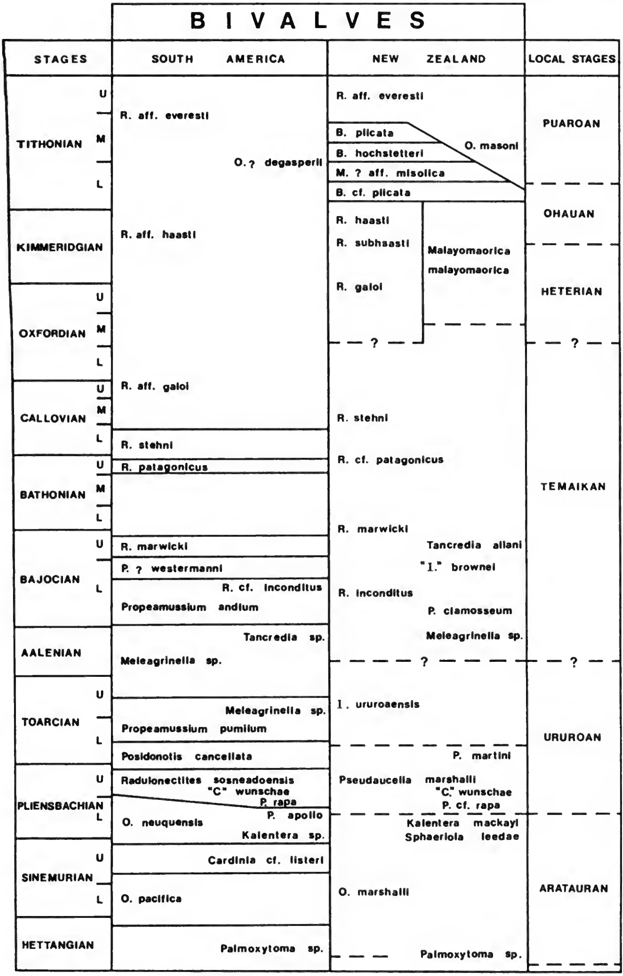
It could be argued by those resorting to some extreme geotectonic reconstructions, such as closure of the Pacific Ocean under an expanding Earth assumption (*cf.* Shields, 1979, fig.1; Ager, 1986; Stevens, 1990, fig.1) or the much more speculative post-Jurassic atomization of a hypothetical Pacifica ancient continent (Nur and Ben-Avraham, 1977, fig. 1), that the paleodistances separating New Zealand from South America might have been very small indeed. Nevertheless, we feel that even within more conventional Gondwanaland reassemblies (*cf.* Quilty, 1982, fig. 82.6; Bradshaw, 1989, fig. 4; Stevens, 1989, figs. 1–3), the paleolatitudes and distances involved seem reasonable enough to account for the faunal links observed. Antarctica, where we might expect to find possible intermediate forms, is an important area for further research, especially since its bivalve faunas have only been analyzed biogeographically for the late Jurassic-Cretaceous interval (Crame, 1986, 1987).

Although no faunas from the Torlesse terrane have been included in this report, it may be worth recalling that within a group of specialized, cemented brachiopods such as the thecideaceans, the first Mesozoic representatives outside Europe-Africa, have only recently been independently discovered in undefined Mid (or Early ?) Jurassic allochtonous rocks from the North Canterbury area (Maxwell, 1987) and in Early Jurassic deposits from west-central Argentina (Manceñido and Damborenea, 1990). Although specimens from the two areas do not appear strictly comparable in detail, it is interesting that they belong to a group usually regarded as indicating warm-temperate waters, dimly lit habitats, specially of reef environments. This stresses the presence of Tethyan affinities as pointed out by Grant-Mackie (1985) and Stevens (1989, 1990).

Biostratigraphy

A correlation chart for the Jurassic of both regions based on their bivalve faunas is offered here (Table 1) in the hope of promoting further discussion on this subject. A more general

Table 1 – Correlation chart between South American and New Zealand Jurassic faunal successions according to marine bivalves.



Dib. C R Tremouilles

approach to a circum-Pacific correlation has been compiled by Damborenea (in press c and in Damborenea *et al*, in press). From a biostratigraphical point of view, the faunal elements in common between the New Zealand and Andean Jurassic add to the debate on the problem of the worldwide correlation of New Zealand Jurassic local stages, which are mostly based on bivalves.

This is best exemplified for the Lower and Middle Jurassic. In the Lower Jurassic there are many species in common. The vertical range of these species is well-known in the Andes (Damborenea in Riccardi *et al*., 1990a). Although we could expect slight differences from one region to the other according to the different taxa involved, we believe these are not significant, whereas the similarities allow a relatively sound basis for correlation with the international Stages (see Table 1).

In the Middle/Upper Jurassic the existence of successive lineages (*R. patagonicus* – *R. stehni* below and *R. galoi* – *R. haasti* above) that repeat general morphological trends are now known to occur at least in South America and in New Zealand. Extreme caution must be taken when referring fragmentary material to any of the species involved from these and other intermediate regions. Biogeographic, evolutionary and taxonomic generalizations must be limited to reasonably well preserved material. From the New Zealand point of view, awareness of this fact will greatly assist in understanding the stratigraphy of Middle and Upper Jurassic deposits. It is especially relevant to the question of definition and correlation of the Temaikan – Heterian boundary.

ACKNOWLEDGEMENTS

The Royal Society of New Zealand generously supported this project with a grant towards living and travel expenses within New Zealand through the "Prince and Princess of Wales Science Award" scheme. The Antorchas Foundation (Argentina) funded the return air fare for Miguel Manceñido and the Museo de La Plata Foundation, through the La Plata agent of Aerolineas Argentinas, provided a return air ticket for Susana Damborenea. All these institutions are gratefully acknowledged.

Many colleagues have greatly helped to make the journey both fruitful and pleasant and to extend a planned two months stay to three months: J. Douglas Campbell, Daphne and William Lee (Dunedin); Alan and Barbara Hoverd (Wellington); Hamish J. Campbell (Lower Hutt); David and Lydia MacKinnon, John D. Bradshaw (Christchurch); Jack and Diana Grant-Mackie; Francis and M. Hirsch; H. Kobe (Auckland). Thanks are extended to other paleontologists and curators who were most helpful, sparing no effort in easing access to many fossil collections, and to satisfy spontaneously various sorts of ancillary needs, particularly Ewan Fordyce and Andrew Grebneff (Dunedin), Don MacFarlan (Nelson), Graeme Stevens and Ian Keyes (Lower Hutt), Margaret Bradshaw (Christchurch) and Joan Sutherland and Neville Hudson (Auckland).

Further technical assistance received from other staff members at Otago University, Auckland University, Canterbury University, New Zealand Geological Survey and Victoria University, is likewise duly appreciated.

The final manuscript benefited from criticism and improvements suggested by A.C. Riccardi, J.D. Bradshaw, D.V. Ager, J.A. Grant-Mackie, J. Begg, G.R. Stevens and J.D. Campbell.

REFERENCES

Ager, D.V., 1986. Migrating fossils, moving plates and an expanding earth. *Modern Geology* 10: 377–390.

Ager, D.V. and Sun, Dongli, 1988. Distribution of Mesozoic brachiopods on the northern and southern shores of Tethys. *Palaeontologia Cathayana* 4: 23–51.

Arkell, W.J., 1956. *The Jurassic Geology of the World*. Oliver & Boyd, Edinburgh and London.

Bayle, E. and Coquand, H., 1851. Mémoire sur les fossiles secondaires recueillis dand le Chili par M. Ignace Domeyko et sur les terrains auxquels ils appartiennent. *Mémoire de la Societé Géologique de France, 2eme série* 4: 1–47.

Bishop, D.G., Bradshaw, J.D. and Landis, C.A., 1985. Provisional terrane map of South Island, New Zealand. In: Howell, D.G. (Ed.): *Tectonostratigraphic Terranes of the Circum-Pacific region*, pp. 515–521. Circum Pacific Council for Minerals and Energy, Houston, Texas.

Boehm, G., 1907. Die Südküsten der Sula-Inseln Taliabu und Mangoli 3. Abschnitt. Oxford des Wai Galo. *Palaeontographica Supplement* 4: 59–120.

Bradshaw, J.D., 1989. Cretaceous geotectonic patterns in the New Zealand region. *Tectonics* 8: 808–820.

Braithwaite, L.R.S., 1984. A contribution to the knowledge of some New Zealand and New Caledonian Triassic and Jurassic Limidae. Unpublished M. Sc. Thesis, University of Auckland.

Bychkov, Y.M., Dagis, A.S., Efimova, A.F. and Polubotko, I.V., 1976. *Atlas triasovoi fauny i flory Severo-Vostoka SSSR*. Izd-vo. 'Nedra', Moskva.

Carter, R.M., 1974. A New Zealand case-study of the need for local time-scales. *Lethaia* 7: 181–202.

Covacevich, V. and Escobar, F., 1979. La presencia del género *Otapiria* Marwick, 1935 (Mollusca: Bivalvia) en Chile y su distribución en el ámbito circumpacífico. *Segundo Congreso Geológico Chileno, Actas* 3: H165-H187.

Cowie, J.W. and Bassett, M.G. (Comp.), 1989. IUGS Global Stratigraphic Chart with geochronometric and magnetostratigraphic callibration. Episodes 12, Suppl.

Cox, L.R., 1961. New genera and subgenera of Mesozoic Bivalvia. *Palaeontology* 4: 592–598.

Cox, L.R. *et al.*, 1969. Mollusca 6. Bivalvia. In: Moore (Ed.): *Treatise on Invertebrate Paleontology. Part N.* I: 1–489; II: 490–952. University of Kansas Press & Geological Society of America. Lawrence, Kansas.

Crame, J. A., 1982. Late Jurassic inoceramid bivalves from the Antarctic Peninsula and their stratigraphic use. *Palaeontology* 25: 555–603.

——— 1984. Preliminary bivalve zonation of the Jurassic Cretaceous boundary. *Memoria del III Congreso Latinamericano de Paleontologia, Mexico* : 242–254.

——— 1986. Late Mesozoic bipolar bivalve faunas. *Geological Magazine* 123: 611–618.

——— 1987. Late Mesozoic bivalve biogeography of Antarctica. Pp. 93–102. In: McKenzie, G.D. (Ed.) Gondwana Six: Sedimentology and Paleontology. American Geophysical Union, Geophysical Monograph 41.

Damborenea, S.E., 1980. Liassic Otapiria (Bivalvia, Monotidae) from west-central Argentina and an account of the distribution of the genus. *Abstracts 5th Gondwana Symposium*: 49.

——— 1982. Revisión de los bivalvos liásicos de la República Argentina. Unpublished Doctoral Tesis, Universidad de La Plata.

——— 1987a. Early Jurassic Bivalvia of Argentina. Part 1. Stratigraphical Introduction and Superfamilies Nuculanacea, Arcacea, Mytilacea and Pinnacea. *Palaeontographica A* 199: 23–111.

——— 1987b. Early Jurassic Bivalvia of Argentina. Part 2. Superfamilies Pteriacea, Buchiacea and part of Pectinacea. *Palaeontographica A* 199: 113–216.

——— 1989. El género *Posidonotis* Losacco (Bivalvia, Jurásico inferior): su distribución estratigráfica y paleogeográfica. *Actas IV Congreso Argentino de Paleontologia y Bioestratigrafia* 4: 45–51.

——— 1990. Middle Jurassic inoceramids from Argentina. *Journal of Paleontology* 64: 736–759.

——— 1991. Early Jurassic Bivalvia of Argentina: Superfamilies Monotacea, Pectinacea and Plicatulacea. Unpublished Ph. D. Thesis, University of Wales, Swansea.

——— in press a. South American Jurassic bivalves. In: Westermann, G.E.G. (Ed.): *Circum Pacific Jurassic, Part 7, Atlas*. Cambridge University Press, Cambridge.

——— in press b. Early Jurassic South American pectinaceans and circum-Pacific palaeogeography. *Palaeogeography, Palaeoclimatology, Palaeoecology.*

——— in press c. Circum-Pacific correlation of Argentine Early and Middle Jurassic bivalve zones. *Geobios* (Third International Symposium on Jurassic Stratigraphy, Poitiers, Sept. 1991; Abstracts: 31).

Damborenea, S.E., Polubotko, I.V., Sey, I.I. and Paraketsov, K.V. (in press). Bivalve Zones and Assemblages of the Circum-Pacific region. In: Westermann, G.E.G. (Ed.): *Circum-Pacific Jurassic*, Chapter 16. Cambridge University Press, Cambridge.

Feruglio, E., 1937. Palaeontographia Patagonica. *Memorie dell' Istituto Geologico della R. Universitá di Padova* 9: 1–384.

Fleming, C.A., 1964. History of the Bivalve Family Trigoniidae in the South-West Pacific. *The Australian Journal of Science* 26: 196–204.

——— 1967. Biogeographic change related to Mesozoic orogenic history in the southwest Pacific. *Tectonophysics* 4: 419–427.

——— 1979. *The geological history of New Zealand and its life.* Auckland University Press, Auckland.

——— 1987. New Zealand Mesozoic bivalves of the Superfamily Trigoniacea. *N. Z. Geological Survey, Paleontological Bulletin* 53: 1–104.

Fleming, C. A. and Kear, D., 1960. The Jurassic sequence at Kawhia Harbour, New Zealand (Kawhia Sheet, N73). *N. Z. Geological Survey, Bulletin* 67: 1–50.

Frebold, H., 1957. The Jurassic Fernie Group in the Canadian Rocky mountains and foothills. *Memoir of the Geological Survey of Canada* 287: 1–197.

——— 1966. Upper Pliensbachian beds in the Fernie Group of Alberta. *Paper, Geological Survey of Canada* 66–27: 1–9.

Fuenzalida R. and Covacevich V., 1988. Vulcanismo y bioestratigrafia del Jurásico superior y Cretácico inferior en la Cordillera Patagónica, región de Magallanes, Chile. *Actas del 5o Congreso Geológico Chileno* 3: H159-H183.

Grant-Mackie, J.A., 1960. On a new *Kalentera* (Pelecypoda: Cypricardiacea) from the Upper Triassic of New Zealand. *N.Z. Journal of Geology and Geophysics* 3: 74–80.

——— 1985. New Zealand – New Caledonian Permian – Jurassic faunas. Biogeography and terranes. *N.Z. Geological Survey, Record* 9: 50–52.

Grant-Mackie, J.A., Hudson, N. and Helby, R., 1986. The Murihiku Callovian – Oxfordian "hiatus" seems to be closed. *Geological Society of New Zealand, Miscellaneous Publications* 35A: 55.

Groeber, P., 1924. Descubrimiento del Triásico marino en la República Argentina. *Comunicaciones del Museo de Historia Natural de Buenos Aires* 2: 87–94.

Hallam, A., 1977. Jurassic bivalve biogeography. *Paleobiology* 3: 58–73.

——— 1983. Early and mid-Jurassic molluscan biogeography and the establishment of the central Atlantic seaway. *Palaeogeography, Palaeoclimatology, Palaeoecology* 43: 181–193.

——— 1986. Evidence of displaced terranes from Permian to Jurassic faunas around the Pacific margins. *Journal of the Geological Society, London* 143: 209–216.

Hayami, I., 1959. Lower Liassic Lamellibranch fauna of the Higashinagano formation in west Japan. *Journal of the Faculty of Science, University of Tokyo, Sec. 2*, 12: 31–84.

——— 1975. A systematic survey of the Mesozoic Bivalvia from Japan. *Bulletin, University Museum, University of Tokyo* 10: 1–249.

Helby, R., Wilson, G.J. and Grant-Mackie, J.A., 1988. A preliminary study of Middle to Late Jurassic dinoflagellate assemblages from Kawhia, New Zealand. *Memoir of the Association of Australasian Palaeontologists* 5: 125–166.

Hölder, H., 1979. Jurassic. In: Robison, R.A. and Teichert, C. (Eds.): *Treatise on Invertebrate Paleontology. Part A. Introduction. Biogeography and Biostratigraphy*, pp. 390–417. Geological Society of America and University of Kansas Press, Lawrence, Kansas.

Howell, D.G., 1980. Mesozoic accretion of exotic terranes along the New Zealand segment of Gondwanaland. *Geology* 8: 487–491.

Hudson, N., 1983. Stratigraphy of the Ururoan, Temaikan, and Heterian Stages; Kawhia Harbour to Awakino Gorge, South-West Auckland. Unpublished M. Sc. Thesis, University of Auckland.

Hudson, N., Grant-Mackie, J.A. and Helby, R., 1987. Closure of the New Zealand 'Middle Jurassic Hiatus' ?. *Search* 18: 146–148.

Imlay, R. W., 1955. Characteristic Jurassic Mollusks from Northern Alaska. *Professional Paper, United States Geological Survey* 274-D: 69–96.

Kiparisova, L.D., Bychkov, Y.M., and Polubotko, I., 1966. *Pozdnetriasovye dvustvorchatye mollyuski Severo-Vostoka SSSR.* Sev.-Vost. Geol. Uprav. (VSEGEI), Magadan.

Levy, R., 1967. Revisión de las Trigonias de Argentina. II. La presencia de *Myophorigonia* en el Lias medio de Neuquén y Chubut. *Ameghiniana* 5: 11–16.

Li, Xiaochi and Grant-Mackie, J.A., 1988. Upper Jurassic and Lower Cretaceous *Buchia* (Bivalvia) from southern Tibet, and some wider considerations. *Alcheringa* 12: 249–268.

MacFarlan, D.A.B., 1985. Triassic and Jurassic Rhynchonellacea (Brachiopoda) from New Zealand and New Caledonia. Unpublished Ph. D. Thesis, University of Otago, Dunedin.

——— 1990. Triassic and Jurassic Rhynchonellacea (Brachiopoda) from New Zealand and New Caledonia. *2nd International Brachiopod Congress, Dunedin, Abstracts*: 63.

Manceñido, M.O., 1978. Studies of Early Jurassic Brachiopoda and their distribution, with special reference to Argentina. Unpublished Ph. D. Thesis, University of Wales, Swansea.

———— 1981. A revision of Early Jurassic Spiriferinidae (Brachiopoda, Spiriferida) from Argentina. In: Volkheimer, W. and Musacchio, E. (Eds.): *Cuencas sedimentarias del Jurásico y Cretácico de América del Sur* 2, pp. 625–659.

———— 1983. A new terebratulid genus from western Argentina and its homoeomorphs (Brachiopoda, Early Jurassic). *Ameghiniana* 20: 347–365.

———— 1990. The succession of Early Jurassic brachiopod faunas from Argentina: correlations and affinities. In: Mackinnon, D.I., Lee, D.E. and Campbell, J.D. (Eds.): *Brachiopods through time*, pp. 397–404. 2nd International Brachiopod Congress, Dunedin.

———— in press. First record of Jurassic nucleatid brachiopods from the SW Pacific, with comments on the global distribution of the group. *Palaeogeography, Palaeoclimatology, Palaeoecology.*

Manceñido, M.O. and Dagys, A.S., in press. Brachiopods. In: Westermann, G.E.G. (Ed.): *Circum Pacific Jurassic. Chapter 22 and Part 7, Atlas*. Cambridge University Press, Cambridge.

Manceñido, M.O. and Damborenea, S.E., 1990. Corallophilous micromorphic brachiopods from the Lower Jurassic of West Central Argentina. In: Mackinnon, D.I., Lee, D.E. and Campbell, J.D. (Eds.): *Brachiopods through time*, pp. 89–96. 2nd International Brachiopod Congress, Dunedin.

Marwick, J., 1953a. Faunal Migrations in New Zealand Seas during the Triassic and Jurassic. *New Zealand Journal of Science and Technology* B 34: 317–321.

———— 1953b. Divisions and Faunas of the Hokonui System (Triassic and Jurassic). *N. Z. Geological Survey, Paleontological Bulletin* 21: 1–142.

Maxwell, P.A., 1987. Square snails, button-shells and jewell-box brachiopods – an unusual faunule from the North Canterbury Torlesse. Programs and Abstracts, Geological Society of New Zealand Miscelaneous Publication 37A: 82.

Milova, L.V., 1976. Stratigrafiya i dvustvorchatye mollyuski triasovo-yurskikh otlozhenii Severnogo Priokhot'ya. *Tr. Sev.-Vost. Kompleksn. Inst., Dal'nevost. Tsentr. Akad. Nauk. SSSR* 65: 1–110. Izd-vo 'Nauka'.

Moericke, W., 1894. Versteinerungen des Lias und Unteroolith von Chile. *Neues Jahrbuch für Mineralogie, Geologie und Paläontologie* 9: 1–100.

Nur, A. and Ben-Avraham, Z., 1977. Lost Pacifica continent. *Nature* 270: 41–43.

Pérez, E. and Reyes, R., 1977. Las Trigonias Jurásicas de Chile y su valor cronoestratigráfico. *Boletin del Instituto de Investigaciones Geológicas, Chile* 30: 1–58.

Philippi, R. A., 1899. *Los Fósiles Secundarios de Chile*. F. A. Brockhaus, Santiago.

Polubotko, I.V., 1968a. Nekotorye pozdnetriasovye *Lima* i *Plicatula* Severo-Vostoka SSSR. Pp. 224–227. In: Markovskii, V.P. (Ed.): *Novye vidy drevnikh rastenii i bespozvonochnykh SSSR.* Vypusk II. Chast' I. VSEGEI, Izd-vo 'Nedra'.

———— 1968b. Dvustvorchatye Mollyuski nizhnei i srednei yury. In: Efimova, A. *et al.*: *Polevoi Atlas yurskoi fauny i flory Severo-Vostoka SSSR*, pp. 29–50, 59–99, tabl.1–8, 21–32, 39–42, 59–66, 70–78, 82–93. Magadans Knizh. Izd-vo.

Polubotko, I.V. and Repin, Y. S., 1988. Lower and Middle Jurassic of the North-East. In: Westermann, G. E. G. and Riccardi, A.C. (Eds.): *Jurassic taxa ranges and correlation charts for the Circum Pacific.* ,pp. 1–17. 1. Soviet Union. Newsletters on Stratigraphy 19.

Purser, B.H., 1961. Geology of the Port Waikato Region (Onewhero Sheet N51). *N.Z. Geological Survey, Bulletin* 69: 1–36.

Quilty, P.G., 1982. Tectonic and other implications of Middle-Late Jurassic rocks and marine faunas from Ellsworth Land, Antarctica. In: Craddock, C. (Ed.): *Antarctic Geoscience*, pp. 669–678. Proceedings of a Symposium on Antarctic Geology and Geophysics, Madison, Wisconsin, 1977.

Riccardi. A.C., 1984. Las asociaciones de amonitas del Jurásico y Cretácico de la Argentina. *Actas del 9o Congreso Geológico Argentino* 4: 559–595.

Riccardi, A.C., Damborenea, S.E. and Manceñido, M.O., 1990a. Lower Jurassic of South America and Antarctic Peninsula. In: Westermann, G.E.G. and Riccardi, A.C. (Eds.): *Jurassic taxa ranges and correlation charts for the Circum-Pacific*, pp. 75–103. Newsletters on Stratigraphy 21.

Riccardi, A.C., Westermann, G.E.G, and Damborenea, S.E., 1990b. Middle Jurassic of South America and Antarctic Peninsula. In: Westermann, G.E.G. and Riccardi, A.C. (Eds.): *Jurassic taxa ranges and correlation charts for the Circum Pacific*, pp. 105–128. Newsletters on Stratigraphy 21.

Riccardi, A.C., Westermann, G.E.G. and Elmi, S., 1990c. The Middle Jurassic Bathonian-Callovian ammonites Zones of the Argentine-Chilean Andes. *Geobios* 22: 553–597.

Riccardi, A.C., Damborenea, S.E., Manceñido, M.O. and Ballent, S.C., 1988. Hettangiano y Sinemuriano marinos en Argentina. *Actas 5o Congreso Geológico Chileno* 2: C359-C373.

——— 1991. Hettangian and Sinemurian biostratigraphy of Argentina. *Journal of South American Earth Sciences* 4: 159–170.

Sey, I.I., 1984. Pozdneplinsbakhkie dvustvorchatye mollyuski Bureinskogo progiba. In: Poyarkova, Z.V., Konovalov, V.P. and Vasil'kovskij, N.R. (Eds.): *Novye dannye po detal'noj biostratigrafii Fanerozoya Dal'nego Vostoka*, pp. 86–96. Akademiya Nauk SSSR, Dal'nevostochyj Nauchnyj Tsentr.

Shields, O., 1979. Evidence for initial opening of the Pacific Ocean in the Jurassic. *Palaeogeography, Palaeoclimatology, Palaeoecology* 26: 181–220.

Skwarko, S.K., 1974. Jurassic fossils of western Australia, 1: Bajocian Bivalvia of the Newmarracarra Limestone and Kojarena Sandstone. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics* 150: 1–53, pl. 21–26.

Speden, I.G., 1970. Three new Inoceramid species from the Jurassic of New Zealand. *N.Z. Journal of Geology and Geophysics* 13: 825–851.

Spörli, K. B. and Grant-Mackie J. A., 1976. Upper Jurassic fossils from the Waipapa Group of Tauharanni Peninsula, North Auckland, New Zealand. *N.Z. Journal of Geology and Geophysics* 19: 21–34.

Stehn, E., 1923. Beiträge zur Kenntnis des Bathonien und Callovien in Südamerica. *Neues Jahrbbuch für Mineralogie, Geologie und Paläontologie, Beilage Band* 48: 52–158.

Stevens, G.R., 1977. Mesozoic biogeography of the Southwest Pacific and its relationship to plate tectonics. In: *International Symposium on Geodynamics in the Southwest Pacific*, pp. 309–326..

——— 1980. Southwest Pacific faunal palaeobiogeography in Mesozoic and Cenozoic times: a review. *Palaeogeography, Palaeoclimatology, Palaeoecology* 31: 153–196.

——— 1989. The nature and timing of biotic links between New Zealand and Antarctica in Mesozoic and early Cenozoic times. In: Crame, J.A. (Ed.): *Origins and Evolution of the Antarctic Biota*, pp. 141–166. Geological Society, London, Special Publication 47.

——— 1990. The Influences of Palaeogeography, Tectonism and Eustasy on Faunal Development in the Jurassic of New Zealand. *Atti del Secondo Convegno Internazionale Fossili, Evoluzione, Ambiente, Pergola* 1988: 441–457.

Stevens, G.R. and Speden, I.G., 1978. New Zealand. In: Moullade, M. and Nairn, A. (Eds.): *The Phanerozoic Geology of the World, II. The Mesozoic*, pp. 251–328. Elsevier.

Tornquist, A., 1898. Der Dogger am Espinazito-Pass, nebst einer Zusammenstellung der jetzigen Kenntnisse von der Argentinischer Juraformation. *Palaeontologische Abhandlung* 4: 135–204.

Trechmann, C.T., 1923. The Jurassic rocks of New Zealand. *Quarterly Journal of the Geological Society, London*, 79: 246–286.

Weaver, C., 1931. Paleontology of the Jurassic and Cretaceous of West Central Argentina. *Memoir, University of Washington* 1: 1–469.

Westermann, G. E. G. and Callomon, J.H., 1988. The Macrocephalitinae and associated Bathonian and early Callovian (Jurassic) ammonoids of the Sula Islands and New Guinea. *Palaeontographica A* 203: 1–90.

Westermann, G.E.G. and Hudson, N., 1991. The first find of Eurycephalitinae (Jurassic Ammonitina) in New Zealand and its biogeographic implications. *Journal of Paleontology* 65: 689–693.

Westermann, G.E.G., Sato, T. and Skwarko, S.K., 1978. Brief report on the Jurassic biostratigraphy of the Sula Islands,Indonesia. *Newsletters on Stratigraphy* 7: 96–101.

Wright, E. and Campbell, J.D., 1990. Mentzelioid brachiopods and the Triassic-Jurassic boundary in the Hokonui Hills, New Zealand. *Abstracts 2nd International Brachiopod Congress, Dunedin*: 102.

Zakharov, V.A., 1962. Novye Monotidae nizhnego leiasa s poberezhyya Okhotskogo morya i ikh stratigraficheskoe znachenie. *Geologiya i Geofizika (Sibirskie Otdelenie)* 1962: 23–31,

Received 31 January 1991; accepted 6 December 1991

© *Journal of the Royal Society of New Zealand,*
Volume 22, Number 2, June 1992, pp 153–156

Greenhouse gas contributions from coal mining in Australia and New Zealand

B.B. Beamish[1] and W.E. Vance[2]

Three important gases commonly associated with coal mining, *i.e.* methane (CH_4), carbon dioxide (CO_2) and carbon monoxide (CO), are recognised as greenhouse gases. In greenhouse gas inventories, estimates of the volume of these gases released by coal mining, particularly methane, appear to be grossly miscalculated. In 1988, 0.8 Mt of underground coal was mined in New Zealand, emitting 12 Gg of methane. In Australia in the same year, two longwall operations emitted 74.3 Gg of methane. Methane from coalseams as an energy resource is being under-utilised.

Keywords: coal mining, gas emission, greenhouse gases

INTRODUCTION

Gas emissions from underground coal mines have been widely researched from the view of safety and productivity (Battino *et al.*, 1988; Hungerford *et al.*, 1988). Methane production from coalseams as an energy resource is also increasingly being examined (Battino *et al.*, 1989; Kuuskraa and Brandenburg, 1989). At some coal mines these two aspects are treated in tandem, to the benefit of the mine operators. More recently, attention has been turned to gas emissions from coal mining as contributions to the production of greenhouse gases, and various estimates have been made as to the volumes involved (Shephard *et al.*, 1982; Pearman and Fraser, 1988; Smith, 1989). Global and local inventories of carbon dioxide, methane and carbon monoxide attributable to coal mining have been based on: (a) material budget analysis for release of CH_4, calculated from tonnes mined and average methane content of the coal (Barns and Edmonds, 1990), and (b) combustion of coal, equating to the release of CO_2 and CO.

The material budget analysis oversimplifies the release of CH_4 from coal mining, and leads to important errors in both global and local inventories. The following discussion reveals the complex nature of coalseam gas emissions, which must be considered when producing gas inventories from coal mining.

RESULTS

Actual gas release mechanisms from coal are multi-phase (Saghafi, 1989; Harpalani and McPherson, 1986; Smith and Williams, 1984), and do not fit standard gas reservoir engineering theories. The gas content of the coalseam being worked is only one factor controlling gas emission into mine workings. Gas from adjacent seams and strata also migrates to the current workings, attracted by the destressing of the surrounding strata, while gas continually escapes into the workings from the exposed coal surfaces of the mine roadways. Finally, gas from the mined coal fragments is liberated at their broken surfaces. Gas from all these sources is released into the ventilation, which contains significantly more gas than stated in the gas emission estimate obtained from the gas content of the seam being worked and tonnes mined.

---

[1] Department of Geology, University of Auckland, Auckland, New Zealand. Present address: Coalseam Gas Research Institute, James Cook University, Townsville, Australia

[2] Department of Mining Engineering, University of Auckland, Auckland, New Zealand

Table 1 – Methane emissions from Australian longwall operations

Colliery	Annual production(Mt)	In-situ gas content (m^3t^{-1})*	Material budget emission estimate ($Ggyr^{-1}$)	Actual methane emission ($Ggyr^{-1}$)
Appin	1.30	15	13.9	55.7
Pacific	0.78	5	2.8	18.6

* 1 m^3t^{-1} = 0.714 kgt^{-1} CH_4

An additional source of gas emission from coal mining is the process of coal oxidation. Mine roadways are subject to this process as soon as the coal is exposed to the ventilating airstream. The result is the escape of CO and CO_2 into the exhaust ventilation. The emission of gas from opencast mining is not considered here, but would usually be negligible as the coal mined is close to the surface and has already been degassed.

Australian collieries

Two examples are presented in Table 1, based on published data from Battino *et al.* (1988). Both mines are operating high production longwall faces. Mining method, and more importantly production rate, play an important role in governing the difference between actual and estimated emissions from material budget analysis. In the examples presented, the material budget approach would have yielded gas emission estimates for Appin Colliery and Pacific Colliery of 1/4 and 1/7 of the actual emission, respectively. These values are similar to those from coal mines in the United States of America (Kissell *et al.*, 1973).

The composition of coalseam gas is dominantly methane, but may also include carbon dioxide (Lama, 1988). At Tahmoor Colliery, New South Wales, Australia, seam gas is composed of variable mixtures of CO_2/CH_4 (Williams *et al.*, 1986). At No. 2 Mine, Collinsville, Queensland, Australia the seam gas is predominantly CO_2 (greater than 95% Beamish *et al.*, 1985). Greenhouse gas inventories do not consider the extra quantities of CO_2 produced by a mixed seam gas (and conversely, the reduced CH_4 content).

New Zealand collieries

Most of New Zealand's underground coal production is from low rank (sub-bituminous) coals, whose gas contents are not high (0–6 m^3/t) compared with overseas coals. The dominant seam gas is methane, with minor proportions of carbon dioxide in some areas. Underground coal production rates are low, and the actual gas emissions are substantially higher than predicted by material budget analyses.

Curl (1978) reviewed work by Noack (1976), which illustrated that there is a relationship between production rate of West German underground coal mines and the actual methane emissions, variable according to gas content. Mine gas emission data for New Zealand coal mines (Beamish and Vance, 1990a) are presented in a similar form in Fig. 1. The diagram illustrates the error introduced by accepting the assumptions of a material budget analysis when predicting methane emissions from coal mining, particularly at low production rates. Coal production from New Zealand underground mining in 1988 was 0.8 Mt. The estimated emission of methane, using the rates from Fig. 1, totalled 12 Gg (Table 2).

The estimated emission of 12 Gg (0.009 × 10^6 tonnes C) is within the recent range quoted by Hollinger and Hunt (1990), (0.004–0.012 × 10^6 tonnes C) and is similar to the result obtained by Lassey *et al.* (1990) (16 Gg), later revised to 5.9 Gg in the light of data presented by Barns and Edmonds (1990) (K.R.Lassey, personal communication, 1990). The methodology of obtaining these values is, however, completely different. This study uses actual mine emission data from operating underground mines, rather than the product of multiplying New Zealands total coal production by a gas content factor. The latter gives equal weighting to both opencast and underground production, which is very misleading.

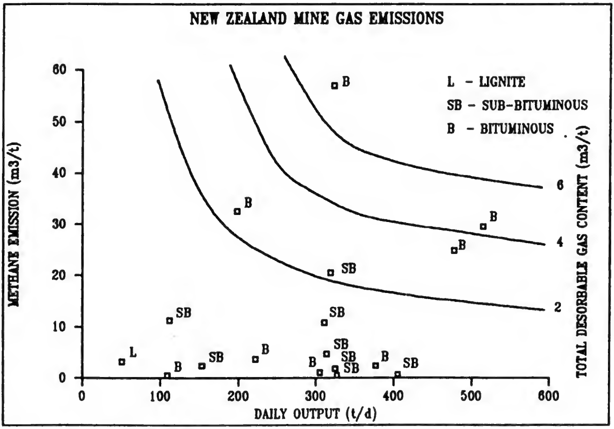


Fig. 1.– Gas emission data from New Zealand coal mines (after Beamish and Vance, 1990a).

CONCLUSIONS

While the process of coal oxidation contributes only a minor component of the overall CO_2 and CO released by coal mining, it is still important to quantify this source. The CH_4 contribution is more significant, as it is commonly recognised that most methane budgets underestimate production from fossil fuel sources (Pearman and Fraser, 1988; Lowe *et al.*, 1988; Sackett and Barber, 1988). The sources of gas emissions outlined here could well account for part of this discrepancy. Also, the common use of the same material budget approach in methane inventories for both opencast and underground coal production is not valid. Recognition of these specific greenhouse gas contributions is necessary before any policy can be formulated for reductions in emissions from coal mining.

New Zealands' contribution to the total global greenhouse gases derived from coal mining are low compared with those of other countries. Methane from New Zealand coal mining in 1988 totalled 12 Gg, estimated from data on mine gas emissions. Actual data from two Australian longwall operations totalled 74.3 Gg of methane emitted from one year's coal production. Australia has 17 active longwall operations , and several of them employ gas drainage techniques to reduce emissions into the workings. The methane contribution from all Australian underground operations requires accurate assessment, if government is to achieve its aim of reducing national levels of greenhouse gas emissions.

Table 2 – Estimated methane emissions from New Zealand coal mining operations

Coal rank	1988 underground production (kt)	Methane emission (Gg)
Bituminous	125	4.41
Sub-bituminous	655	7.93
Total	780	12.34

There is increasing concern over greenhouse gas emissions and their effects, so it is important to pursue the utilisation of methane from coalseams. This non-renewable energy resource provides a cleaner and more efficient fuel. Methane from coalseams has been considered in the past as a safety liability, and now more recently an environmental liability; it can be converted into an asset.

REFERENCES

Barns, D.W. and Edmonds, J.A., 1990. *An evaluation of the relationship between the production and use of energy and atmospheric methane emissions*. United States Department of Energy, Office of Energy Research, Carbon Dioxide Research Program, Washington, D.C. DOE/NBB–0088P.

Battino, S., Lunarzewski, L. and Truong, D., 1988. *Towards a reliable gas emission prediction method for Australian longwall mining*. Proceedings of The AusIMM Illawarra Branch, 21st Century Higher Production Coal Mining Systems – Their Implications, Wollongong, NSW, Australia, pp. 315–322.

Battino, S., Malone, P. and Bishop, R.J., 1989. Coal bed methane extraction and utilisation – the Australian experience. *The Coal Journal*, No.26, 1–9.

Beamish, B.B., Hungerford, F., McKavanagh, B. and Williams, R.J., 1985. Outburst research (Collinsville Coal Co., Queensland (Australia)). NERDDP-EG–85–495 Canberra, ACT, Australia. National Energy Research, Development and Demonstration Council

Beamish, B.B. and Vance, W.E., 1990a. *Gas content of New Zealand coals*. Proceedings of 18th Australasian Chemical Engineering Conference, The University of Auckland, New Zealand, pp. 1116–1123.

———— 1990b. *Gas research at Huntly West Mine, New Zealand*. Department of Mining Engineering, University of Auckland, Technical Report, November 1990, 32p.

Curl, S.J., 1978. *Methane prediction in coal mines*. London, UK, IEA Coal Research, Report No. ICTIS/TR04.

Harpalani, S.H. and McPherson, M.J., 1986. Retention and release of methane in underground coal workings. *International Journal of Mining and Geological Engineering* 4: 217–233.

Hollinger, D.Y. and Hunt, J.E., 1990. Anthropogenic emissions of carbon dioxide and methane in New Zealand. *Journal of the Royal Society of N.Z.*, 20: 337–348.

Hungerford, F., Kelly, M., Saghafi, A. and Williams, R.J., 1988. Long-hole drilling for gas emission control at Appin Colliery, NSW, Australia. Proceedings of Fourth International Mine Ventilation Congress, Brisbane, Queensland, Australia, pp. 207–216.

Kissell, F.N., McCulloch, C.M. and Elder, C.H., 1973. *The direct method of determining methane content of coalbeds for ventilation design*. U.S. Bureau of Mines R.I. 7767.

Kuuskraa, V.A. and Brandenberg, C.F., 1989. Coalbed methane sparks a new energy industry. *Oil and Gas Journal*, Oct 9, 49–56.

Lama, R.D., 1988. Adsorption and desorption of mixed gases on coal and their implications in mine ventilation. Proceedings of Fourth International Mine Ventilation Congress, Brisbane, Queensland, Australia, pp. 161–174.

Lassey, K.R., Lowe,D.C., and Manning, M.R., 1990. *Sources and sinks of atmospheric methane in New Zealand: a perspective*. Institute of Nuclear Sciences, INS-R–419.

Lowe, D.C., Brenninkmeijer, C.A.M., Manning, M.R., Sparks, R. and Wallace, G., 1988. *Radiocarbon determination of atmospheric methane at Baring Head, New Zealand*. Nature 332: 522–525.

Noack, K., 1976. Effect of face length, working speed and type of stowing on methane emission. *Glueckauf* 1976, 112, No. 20: 1156–1159 (in German).

Pearman, G.I. and Fraser, P.J., 1988. Sources of increased methane. Nature, 332, 489–490.

Sackett, W.M. and Barber, T.R., 1988. Fossil carbon sources of atmospheric methane. *Nature* 334: 201.

Saghafi, A., 1989. A computer simulation of gas flow in coal seam and its application to long borehole drainage pattern design. Proceedings of Computer Systems in the Australian Mining Industry, The University of Wollongong, Australia, pp. 218–226.

Shephard, J.C., Westburg, H., Hopper, J.F., Ganesan, K. and Zimmerman, P.J., 1982. Inventory of global methane sources and their production rates. *Geophysical Research* 87: No.C2, 1305–1312.

Smith, D.M. and Williams, F.L., 1984. Diffusion models for gas production from coal. *Fuel* 63: 256–261.

Smith, I.M., 1989. The greenhouse effect and the role of coal. Proceedings of Third Coal Research Conference, Wellington, New Zealand, pp. 1–12.

Williams, R.J., Allen, J., Truong, D., Beamish, B.B. and Hungerford, F., 1986. An evaluation of seam gas drainage by longhole drilling. *The Coal Journal*, No.10, 13–22.

Received 15 March 1991; accepted 20 December 1991

*© Journal of the Royal Society of New Zealand,
Volume 22, Number 2, June 1992, pp 157*

CORRECTION

In the paper by R.L. Palma, "A new species of *Rallicola* (Insecta: Phthiraptera: Philopteridae) from the North Island brown kiwi", (in *The Journal of the Royal Society of New Zealand*, Volume 21, Number 4, December 1991, pp 313-322), a typesetting code denoting the male and female symbols was accidentally cancelled. The places where these symbols were intended to appear were occupied instead by the letters A and B, respectively.

The Royal Society regrets this error.